

THE EUROPEAN SPECIES OF THE CRETACEOUS AMMONITE *ROMANICERAS* WITH A REVISION OF THE GENUS

by W. J. KENNEDY, C. W. WRIGHT, and J. M. HANCOCK

ABSTRACT. The genus *Romaniceras* Spath, 1923, is shown to be a member of the subfamily Euomphaloceratinae Cooper, 1978, derived probably from *Kamerunoceras* Reyment, 1954. Three subgenera are recognized: *R. (Romaniceras)*, *R. (Yubariceras)* Matsumoto, Saito, and Fukada, 1957, and *R. (Obiraceras)* Matsumoto, 1975. The European Turonian yields three successive species: *R. (R.) kallesi* (Zázvorka), of which *R. hispanicum* Wiedmann is a synonym; *R. (Y.) ornatissimum* (Stoliczka), of which *R. (Y.) deverioides* (de Grossouvre) and *R. (Y.) yubarensis* Matsumoto, Saito, and Fukada are the most important synonyms; and *R. (R.) deverianum* (d'Orbigny) of which *R. (R.) uchauxiense* Collignon, *R. (R.) medlicottianum* (Stoliczka), *R. (R.) pseudo-deverianum* (Jimbo), and *R. (R.) yezoense* Matsumoto are the most important synonyms.

Dimorphism is tentatively recognized in *R. (Y.) ornatissimum*, and it is shown that there is a high degree of intraspecific and ontogenetic variability in both *R. (Y.) ornatissimum* and *R. (R.) deverianum*, comparable to that seen in other acanthocerataceans.

ROMANICERAS Spath, 1923, is a widespread and frequently quoted genus of multituberculate acanthoceratids of world-wide distribution and of great importance in the correlation of mid and late Turonian successions. This is especially true in Touraine, the type area of the Turonian stage (see discussion in Hancock, Kennedy, and Wright 1977) whilst the genus also provides a link between the collignoniceratid-dominated faunas of Europe and north America and those of more southerly areas dominated by pseudotissotiids and vascoceratids. A considerable number of species has been erected and referred to the genus, although re-examination of the type material of the older European species, such as *Romaniceras deverianum*, shows that many of these are unnecessary. Moreover, various other genera and subgenera have been created for Turonian multituberculate forms and the assignment of species to these varies widely. A revision of the rich European faunas, especially those of Touraine and Uchaux (Vaucluse), is thus long overdue in order to clarify the relationships of the numerous Japanese, American, and other species, as well as to provide a firmer basis for the subdivisions and correlation of the Turonian stage.

SYSTEMATIC PALAEOLOGY

Dimensions. Dimensions of specimens are given in millimetres, in the following order: diameter (D), whorl breadth (Wb), whorl height (Wh), and breadth of umbilicus (U). C and IC refer to costal and intercostal dimensions. Figures in parentheses refer to dimensions as a percentage of diameter.

Suture terminology. The suture terminology of Wedekind (1916; see Kullmann and Wiedmann 1970) is followed in the present work, where I = Internal lobe, U = Umbilical lobe, L = Lateral lobe, E = External lobe.

Techniques. Specimens were photographed on Kodak Pan F 35 mm film, ASA rating 50, using a Pentax reflex camera with a 1:2/55 super Takumar lens. In many cases whitening before photography was found to be unnecessary, especially with Tuffeau specimens.

Suture lines were drawn using a Wild Binocular Microscope with *camera lucida* attachment.

Abbreviations used for collections. AM, Musée de Paléontologie d'Angers; BMNH, British Museum (Natural History), London; EMP, Ecole des Mines, Paris (now housed at the Université Claude Bernard, Lyon); FSL, Faculté des Sciences, Université Claude Bernard, Lyon; FSM, Faculté des Sciences, Le Mans; chiefly collections formerly housed in the Musée de Tessé, Le Mans; FSR, Institut de Géologie, Université de Rennes; GK, Department of Geology, Kyushu University, Fukuoka; GT, University of Tokyo Museum; LC, Lecoindre collection in

the Chateau du Grand-Pressigny, Indre-et-Loire; MN, Muséum d'Histoire Naturelle, Nantes; MNHP, Muséum National d'Histoire Naturelle, Paris; OUM, University Museum, Oxford; unless stated otherwise, these are collections made by Hancock and Kennedy; SP, Collections of the Sorbonne, now Université de Paris VI; WW, C. W. and E. V. Wright collection.

Superfamily ACANTHOCERATACEAE de Grossouvre, 1894

Family ACANTHOCERATIDAE de Grossouvre, 1894

Subfamily EUOMPHALOCERATINAE Cooper, 1978

Genus ROMANICERAS Spath, 1923

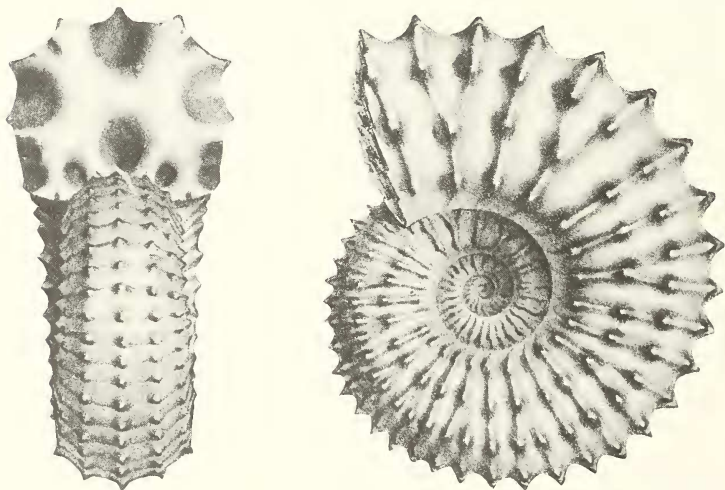
Type species. *Ammonites deverianus* d'Orbigny, 1841 by the original designation of Spath 1923.

Diagnosis. Rather variable acanthoceratids that are evolute and medium sized to large. Whorl sections are moderately compressed to moderately depressed, quadrate or rounded. Early whorls are smooth and bear periodic constrictions with associated ribs. Middle growth stages have long ribs bearing nine, eleven, or thirteen rows of tubercles of unequal strength and spacing. The nine rows are umbilical, lateral, inner and outer ventrolateral, and siphonal; in species with eleven rows the inner ventrolateral may be doubled and in those with thirteen rows, both inner and outer ventrolateral may be doubled at some stage in ontogeny. Short ribs are intercalated on the flank and bear a full ventrolateral complement of tubercles, with or without laterals. Ribs may also bifurcate from the lateral tubercle.

At maturity some or all tubercles are lost; ribs become mainly long and strong and pass uninterrupted across the venter.

The suture line is relatively simple and of basic *Acanthoceras* type, with broad bifid saddles and narrow lobes; all elements have only minor incisions.

Discussion. Spath did not give a diagnosis of this genus. The stability of the genus and the differentiation of its constituent species depend essentially on the interpretation of the type species *Ammonites deverianus* d'Orbigny (1841, p. 356, pl. 110, figs. 1-2) (reproduced here as text-fig. 1):



TEXT-FIG. 1. *R. (Romaniceras) deverianum* (d'Orbigny). Copy of d'Orbigny's original photograph (1841, pl. 110, figs. 1-2), based on specimens from Uchaux, Vaucluse.

'whilst for *A. deverianus* d'Orbigny ... generally erroneously included in *Acanthoceras*, the new genus *Romaniceras* is proposed' (Spath 1923, p. 144). The original description and figures, though the latter are as usual no doubt synthetographs, are perfectly clear, and the species is said to be characterized by its inflation and by nine rows of tubercles, while the only locality mentioned is Uchaux (Vaucluse), with specimens in the collections of Requier, Renaux, Matheron, and d'Orbigny. The original type series therefore can only include Uchaux specimens with nine rows of tubercles in these four collections. Despite this obvious fact, attempts have been made to fix types on different bases.

Basse (1937, pp. 180–181) reported that the Renaux collection, which included a specimen stated by d'Orbigny (1841, p. 357) to be jointly with his the basis of his plate 110, figs. 1, 2, had disappeared. Therefore she endeavoured to clarify the situation by considering what specimens survived in the d'Orbigny collection. She said that the one Uchaux specimen preserved in d'Orbigny's collection (in the Muséum d'Histoire Naturelle, Paris), no. 6781, labelled 'T' for type, was a very badly preserved internal mould from which it was impossible to draw up any list of characters. She also found two other specimens, 6781a from Poncé, Sarthe, and 6781b, from Montrichard, Loir-et-Cher, which she called co-types. Since they are not from Uchaux, they cannot be 'co-types'; nor are a further two specimens from Poncé numbered 6781a and one from Tourtenay labelled 6781c in the d'Orbigny collection. These specimens were probably added to d'Orbigny's collection after 1841 and before it was catalogued in 1858–1860.

Faced with the absence of any good Uchaux specimen, Basse said that she proposed to take the 'co-types' in future as types, and she refigured them (Basse 1937, pl. 8, figs. 1a–b, 2a–b; see Pl. 48, figs. 3–4). Subsequently, Collignon (1939, p. 36) recognized that Basse's so-called co-types were not specimens of *Romaniceras deverianum*, having eleven rather than nine rows of tubercles, and belonged to *R. deverioides* (de Grossouvre). He, therefore, designated as lectotype the original of his pl. 9, fig. 1, 1a; pl. 8, fig. 2. This specimen from Masiaposa, Madagascar, is clearly also not available for lectotype designation.

The surviving Uchaux specimen in the d'Orbigny collection is illustrated here as Pl. 41, figs. 3–4. It is in the typical Uchaux preservation of red-brown silicified rock, and has the appearance of having lain exposed for many years, since it has been converted to a cinder-like porous cast. Only half a whorl is preserved, with the following dimensions: D (estimated) = 49 mm (100); Wb = 29 mm (0.59); Wh = 22 mm (0.45); U = 16 mm (0.33); Wb:Wh = 1.31.

There are fifteen sharp bullae on the umbilical shoulder, each giving rise to a single rib, but it is not possible to determine directly the number present over the venter. Each rib arises at the umbilical seam and passes backward across the umbilical wall to develop into a sharp bulla which projects into the umbilicus. The flanks of the specimen are badly corroded; no single rib is preserved for the whole width. They are, however, initially radial and then flex gently backwards. No lateral tubercles are preserved and only one inner ventrolateral. Three, possibly four ribs are preserved in the outer ventrolateral region, and, if interpreted as tubercles, they are bullate rather than clavate. Five, possibly six, siphonal tubercles are preserved and these appear to have been rounded. There are thus at the most seven rows of tubercles preserved on the specimen. Since this specimen is from Uchaux, it is obviously a *Romaniceras*, while the whorl section, and in particular the umbilical bullae, are quite distinctive. It is, however, so poor that it can scarcely have served as the basis for d'Orbigny's figure. It is available for lectotype designation, but it would in our view be injudicious to designate so poor a specimen.

Of the remaining collections that include syntypes, the Matheron collection, preserved in the collections of the Muséum d'Histoire Naturelle, Marseille, suffered greatly in the last war; and we were unable to find specimens of Uchaux *Romaniceras* during a visit made in 1971. The Requier collection is preserved in the Musée d'Avignon, but Roman and Mazeran (1913) make no mention of any surviving *Romaniceras*. The collections of Prosper Renaux, thought by Basse in 1937 to be lost, in fact survive in the collections of the Faculté des Sciences, Montpellier. Dr. J. Sornay informs us that some years ago he saw two poor *Romaniceras* in the Renaux collection; one of them was larger than that indicated by d'Orbigny and a slimmer form than that illustrated (= '*R. uchauxiense*' Collignon); the other showed sutures, which d'Orbigny specifically mentions as being unknown ('tous les

échantillons étant pourvus de leur test, il m'a été impossible de les distinguer. J'ai pu seulement apercevoir, par le dessus de la bouche, qu'il y a extérieurement deux lobes de chaque côté du lobe dorsal, et intérieurement un lobe latéral, de chaque côté du lobe ventral'). These specimens have since disappeared but may turn up again.

In all these circumstances it is undesirable to designate a lectotype immediately. The species meanwhile can be perfectly well interpreted from d'Orbigny's description and figures.

From this position a preliminary review of the Turonian multituberculate forms shows that the majority are readily divisible into two groups, one with nine rows of tubercles and the other with eleven. Most of the former are currently placed in *Romaniceras* sensu stricto, but a few in *Yubariceras* Matsumoto, Saito and Fukada, 1957 (type species *Y. yubarensis* Matsumoto, Saito, and Fukada, 1957, p. 27, pl. 8, fig. 1a-b; pl. 10, fig. 1a-b; pl. 11, fig. 1a-b; pl. 13, fig. 1a-b; pl. 15, fig. 1; text-figs. 8, 9. See Pl. 40, figs. 3-5). Of the species with eleven rows, most have been assigned to *Yubariceras*. Matsumoto *et al.* regarded *Yubariceras* and *Romaniceras* as superficially homoeomorphous offshoots, *Yubariceras* derived from *Calycoceras* of the *newboldi* (Kossmat) group (= *Newboldiceras* Thömel, 1972) (Mantelliceratinae) and *Romaniceras* from *Acanthoceras* (Acanthoceratinae) respectively. They separated the two genera on the basis of *Yubariceras* having quadrate whorls, a rather flat, broad venter, subparallel and less inflated flanks, and tubercles predominant over the ribs, which weaken with growth. Subsequently Matsumoto (1975, pp. 131 *et seq.*) added to the diagnosis the presence of intercalated ventral ribs and constrictions on juvenile whorls. From an examination of the described *Yubariceras* species we find that these characters do not occur together sufficiently consistently to allow us to maintain them as the basis of a separate genus. *R. deverianum* has constricted inner whorls; there is great intraspecific variation in the relative dominance of ribs and tubercles and rectangular whorled individuals were described both by Sharpe (1857, p. 46, pl. 19, fig. 5a-b) and Roman and Mazeran (1913, pl. 3, fig. 2, 2a). The only consistent difference that we can apply is the presence of nine rows of tubercles in one group of species and eleven in another. We cannot support the phylogenetic argument for the independent origin of the two groups. The latest *Calycoceras* (*Newboldiceras*) and *Acanthoceras* of the *rhodomagense* (Brongniart) group considered ancestral date from early in the Late Cenomanian, and there is a considerable gap in the record before the first *Romaniceras* from the middle Turonian (Cooper 1978). On the other hand, constrictions on the inner whorls and multituberculation are seen to occur in the *Euomphaloceras*-*Kamerunoceras* lineage which extends from the Middle Cenomanian to early in the mid Turonian. We have, for instance, a constricted *Kamerunoceras* from the Upper Cenomanian of Shapwick Grange, Devon, near Lyme Regis, which, together with the '*Kanabicerias*' of Freund and Raab (1969, p. 9, pl. 1, figs. 3-6; text-fig. 4d-f) from the 'early Turonian' of Israel, support this link. The earliest whorls of *K. eschii* (Solger) (1904, pl. 4, fig. 2a-b) are smooth and constricted as in *Romaniceras*, whilst the earliest *Romaniceras*, *R. kallesi* Zázvorka, described below, is slowly expanding and evolute—the over-all shell form, in other words, of a *Kamerunoceras* combined with the decoration of a *Romaniceras*. That there are rare individuals (to be described below) which link the nine- and eleven-row species further confirms them as a monophyletic group within the Euomphaloceratinae, as Cooper (1978) has hinted.

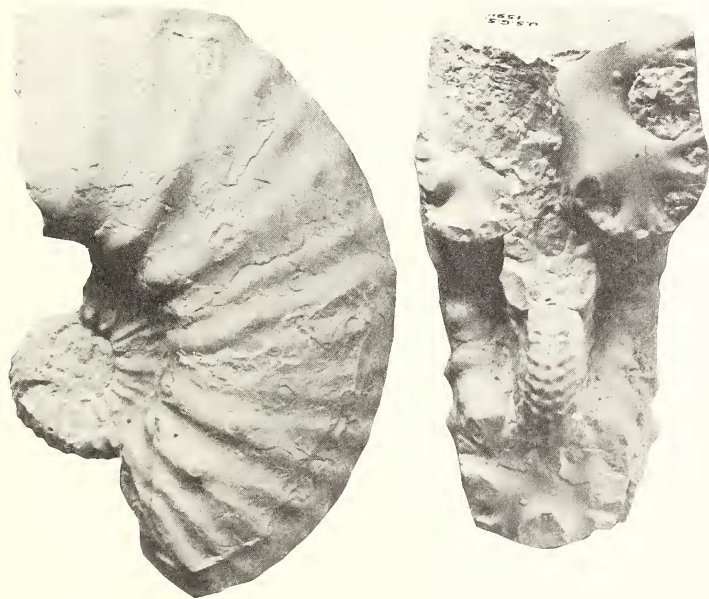
For the record we would note that the Upper Cenomanian *Romaniceras* from the Isle of Wight recorded by Wright and Wright (1951) and cited by Matsumoto as providing an apparent link between the Turonian species and their possible Cenomanian antecedents must be discounted. This specimen (C. W. and E. V. Wright collection no. 10206, loose, ex Middle Cenomanian Lower Chalk, Compton Bay, Isle of Wight, Hampshire) has the inner whorls of a typical *C. (N.)* of the *newboldi* group but the umbilical bullae are displaced outwards to an inner lateral position as size increases, as in *C. (N.) newboldi spinosum* (Kossmat) or *C. (N.) orientale* Matsumoto, Saito, and Fukada. On the outer, but still septate, whorl, a new bulla develops at the umbilical shoulder, and blunt tubercles develop on the ventrolateral shoulder of one flank to give a *Romaniceras*-like appearance to one side of the specimen. This is presumed to be a minor growth disturbance only.

Obiraceras Matsumoto, 1975 (type species *O. ornatum* Matsumoto, 1975, p. 150, pl. 23, fig. 1; text-fig. 18) was characterized by the doubling of both inner and outer ventrolateral nodes in middle growth (Pl. 40, figs. 1, 6), but is otherwise identical to *Yubariceras*.

These three taxa do not merit separation as genera, given the scale of generic division recognised within the Acanthoceratidae (Wright in Arkell 1957). The differences between the three which can be most consistently applied are the numbers of rows of tubercles and it could be argued that these might be no more than specific criteria. However, the same criteria have been consistently and successfully applied to both Acanthoceratinae (e.g. *Calycocheras*) and Texanitinae (e.g. *Texanites*, *Paratexanites*). The recognition of subgenera *R. (Romaniceras)*, *R. (Yubariceras)* and *R. (Obiraceras)* is proposed both as a natural grouping of species and as based on what have proved to be taxonomically useful criteria elsewhere in the Acanthoceratidae.

Comparisons with other genera. *Romaniceras* are easily distinguished from superficially similar Cenomanian genera such as *Acanthoceras* and *Calycocheras* by the presence of additional rows of tubercles in middle and later growth and by smooth, constricted early whorls.

Shuparoceras Matsumoto, 1975 (type species *S. yagii* Matsumoto, 1975, p. 110, pl. 12, fig. 1, text-fig. 3) is a Turonian genus apparently very close to *Romaniceras*; it should perhaps be treated as a further subgenus. It has a compressed, involute shell with high whorls and ornament of long ribs with nine rows of tubercles during middle growth stages, but has broad, low ribs on which all tubercles are very much reduced at maturity. We figure here an undescribed American form from New Mexico which shows it to have had constricted inner whorls, thus confirming the close affinity (text-fig. 2).



TEXT-FIG. 2. *Shuparoceras* sp. nov. Plaster cast of a specimen (15947) in the U.S. Geological Survey Collections, Denver, from the mid Turonian *Prionocyclus hyatti* Zone, 46 km north-west of Albuquerque, New Mexico. Specimen shows inner whorls with constrictions, and the distinctive feebly ornamented outer whorls of the genus. (Courtesy of W. A. Cobban, Denver.)

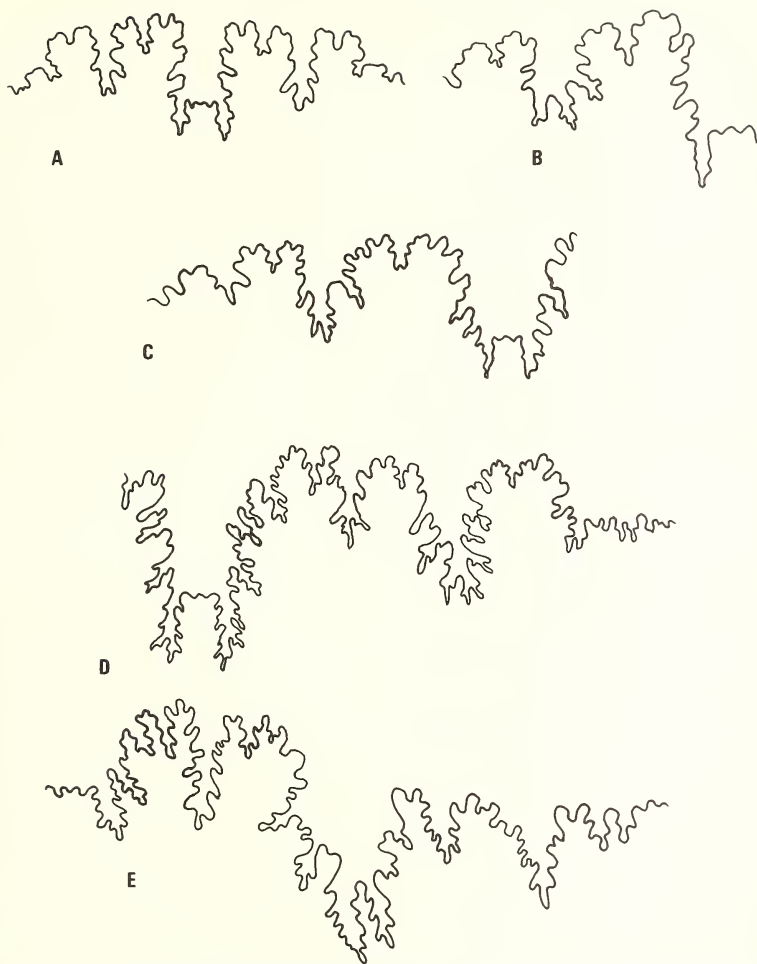
Kamerunoceras Reymont, 1954 (type species *Acanthoceras eschii* Solger, 1904, p. 124, pl. 4, figs. 1–4) are typically very evolute, slowly expanding, and almost serpentine with a polygonal whorl section; they either lack a mid-lateral tubercle, having only seven rows in all (as in the type species), or the tubercle in this position is an umbilical one which has migrated outwards during ontogeny. Furthermore, the siphuncle lies close to the surface producing a low rounded siphonal ridge. The number of siphonal tubercles may exceed the ventral, and ventral ribbing tends to be irregular in many species. We regard *Schindewolfites* Wiedmann, 1960 as a synonym of *Kamerunoceras* (see Kennedy and Wright 1979).

Less readily resolved is the relationship between *Romaniceras* and the poorly known *Tunesites* Pervinquier, 1907. The type species of this genus, *T. salammbo* Pervinquier (1907, p. 255, pl. 12, figs. 5a–b, 6a–b; text-fig. 101) is based on a pyritic nucleus from the ‘Cénomanien ou, à la rigueur, du Gault supérieur du Dj. Guern Halfaya pied N-W, non loin d’Henchrir er Ressay’, Tunisia. The specimen, refigured here as Pl. 39, figs. 19–23, is only 16 mm in diameter but exquisitely preserved. Its inner whorls are smooth, evolute, with a compressed, rounded whorl, but at approximately 8 mm diameter a strong prorsiradiate constriction develops, flanked by distinct collar-ribs. There are three such constrictions on the outer whorl, with progressively stronger collars, and low, irregular ribs develop on the flanks between constrictions, with progressively stronger and more numerous obliquely placed ventral tubercles developing as size increases. The venter changes from rounded to weakly fastigiate from the second constriction, with the development of a low siphonal ridge. Low ribs form a chevron linking the ventral tubercles to this ridge, with siphonal clavi developed at the peak of the chevron on the ridge. The suture line (text-fig. 3A) includes broad, little incised saddles and much narrower lobes. *T. choffati* Pervinquier (1907, p. 257, pl. 12, figs. 7a–b, 8a–b; text-fig. 102; see Pl. 39, figs. 11–16; text-fig. 3B) has, as Pervinquier noted (1907, p. 257), identical innermost whorls, and he thought that perhaps they represented no more than variants of one species. The chief differences are *T. choffati*’s much earlier acquisition of constrictions and associated collars and much stronger flank ribs between, even at an early stage. The smaller paratype (Pl. 39, figs. 11–14) shows no trace of ribs or tubercles on the venter. In contrast, the larger holotype (Pl. 39, figs. 15–16) has flexuous primary ribs which sweep forwards across the venter at only 10 mm diameter and rapidly develop umbilical bullae, conical inner and outer ventrolateral and clavate siphonal tubercles borne on what are exclusively primary ribs; a radially elongate lateral tubercle appears at a somewhat greater diameter. The suture differs from that of the type *T. salammbo* (text-fig. 3B) in having a broader and deeper L. Unlike the poorly dated type of *T. salammbo*, this species, which comes from Koudiat el Hamra, is from a level, ‘sensiblement au niveau de *Forbes. obtectum*’—that is to say probably Middle Cenomanian. The smaller paratype is from A. ez Zerga, ‘*mais son étiquette indique le Turonien (avec un point d’interrogation)*’ (our italics).

Only Pervinquier’s labels now survive with these specimens, but it appears that he may not himself have collected them, for as he indicates in the introduction to his memoir, he was given many specimens by Flick, Thomas, and Peron to use in his work. We would therefore conclude that all these specimens, dated as anything from Albion to Turonian, cannot all be accepted as definitely Cenomanian.

The holotype of *T. salammbo*, with only ventrolateral and siphonal tubercles developed, could be the nucleus of a *Houreceras* Collignon, 1939 (see, e.g., Pl. 39, fig. 24); or a *Kamerunoceras* (see, e.g., Solger 1904, p. 124, pl. 4, figs. 1–4), the nucleus of the type specimen of the type species of which is smooth and round-whorled and develops one constriction with feeble collars at a similar size to *T. salammbo*; or a *R. (Romaniceras)* (e.g. Pl. 39, figs. 7–10) or a *R. (Yubariceras)* (e.g. Pl. 40, fig. 1). In contrast, *Euomphaloceras* is already strongly ribbed and tuberculate at this size. It is therefore clear that *Tunesites* must be treated as a *nomen dubium* since the type is too small to be generically determinable. In contrast, the holotype of *T. choffati*, with its full complement of umbilical, lateral, inner and outer ventrolateral and siphonal tubercles, is a *R. (Romaniceras)*, and probably *R. (R.) devierianum*.

That this circuitous elimination of *Tunesites* is not mere special pleading is confirmed by the recognition that *Eucalyoceras constrictum* Spath, 1926 (= *Acanthoceras* aff. *A. Newboldi* Kossmat



TEXT-FIG. 3. External sutures of *Tunesites* and *Romaniceras*. A. *Tunesites salammbo* (Pervinquier); holotype, $\times 6$. B. *Tunesites hoffati* (Pervinquier); holotype, $\times 6$. C. *Romaniceras* (*Yubariceras*) *ornatissimum* (Stoliczka); GK H5685, $\times 3$. D. *Romaniceras* (*Romaniceras*) *deverianum* (d'Orbigny); the lectotype of *Ammonites medlicottianus* Stoliczka, $\times 1$. E. *Romaniceras* (*Yubariceras*) *ornatissimum* (Stoliczka); the holotype, $\times 1$. (A-B, after Pervinquier, 1907; C, after Matsumoto, 1975; D, E, after Stoliczka, 1865).

of Pervinqui re, 1910, p. 45, pl. 4, fig. 37), based on a small pyritic specimen in the Peron collection (but collected by Thomas) and said to be from the Middle Cenomanian of Berrouaghia, Algeria, is also a *R. deverianum* (Pl. 39, figs. 7–10). It has a smooth, constricted initial stage with collars, then develops flexuous long ribs with a full complement of nine rows of tubercles over the last half-whorl. The intermediate stage, although crushed and distorted, shows umbilical bullae and ventral tubercles to be the first to develop, with a broad, smooth venter, in contrast to the early appearance of siphonal tubercles in *T. salammbo*.

Occurrence. The main occurrence of *Romaniceras* is in the middle part of the Turonian stage; the earliest dated occurrence known to us is in the St. Cyr-en-Bourg Fossil Bed of Touraine (Hancock, Kennedy, and Wright 1977). It also extends to the upper Turonian in Japan. The geographic distribution includes England and France, Czechoslovakia (Bohemia), the Middle East (Israel, Lebanon), Algeria, Tunisia, Nigeria, Madagascar, southern India, Japan, British Columbia, Oregon, California, the western interior of the United States, Texas, and Mexico.

Subgenus *Romaniceras* (*Romaniceras*) Spath, 1923
[= *Proromaniceras* Wiedmann, 1960]

Romaniceras (*Romaniceras*) *deverianum* d'Orbigny

Pl. 39, figs. 7–10; Pl. 41, figs. 1–6; Pl. 42, figs. 1–7; Pl. 43, figs. 1–3; text-figs. 1, 3d, 4, 5

- 1841 *Ammonites deverianus* d'Orbigny, p. 346, pl. 110, figs. 1–2.
1850 *Ammonites Deverianus* d'Orbigny, p. 189.
1857 *Ammonites deverianus* d'Orbigny; Sharpe, p. 43, pl. 19, fig. 5a–b.
1865 *Ammonites medicottianus* Stoliczka, p. 77, pl. 43, fig. 1–1b.
1872 *Ammonites Deverianus* d'Orbigny; Fritsch, p. 32, pl. 7, figs. 4–5.
1894 *Acanthoceras pseudodeverianum* Jimbo, p. 178, pl. 21, fig. 1–1b.
1897 *Acanthoceras Medicottianum* Stoliczka; Kossmat, p. 16.
?1907 *Tunesites Choffati* Pervinqui re, p. 257, pl. 12, figs. 7a–b, 8a–b; text-fig. 102.
1910 *Acanthoceras* aff. *A. Newboldi* Kossmat; Pervinqui re, p. 45, pl. 4, fig. 37.
1913 *Acanthoceras deverianum* d'Orbigny; Roman and Mazeran, p. 25, pl. 3, figs. 1, 1a, 2, 2a;
? text-fig. 4.
1923 *Ammonites deverianus* d'Orbigny; Spath, p. 144.
1926 *Eucalycoceras constrictum* Spath, p. 431.
non 1937 *Acanthoceras deverianum* Basse, non d'Orbigny, p. 180, pl. 8, figs. 1a–b, 2a–b (= *R. (Y.) ornatissimum* (Stoliczka)).
1939 *Romaniceras deveriai* d'Orbigny; Collignon, p. 93, pl. 8, figs. 2, 3–3a; pl. 9, fig. 1–1a.
1939 *Romaniceras deveriai* d'Orbigny var. *masiaposensis* Collignon, p. 89, pl. 9, figs. 2, 2a–b.

EXPLANATION OF PLATE 39

All figures are $\times 2$.

Figs. 1–6, 17–18. *R. (Yubariceras) ornatissimum* (Stoliczka). Early developmental stages of OUM KT 993 from the mid Turonian of Swede Creek, Shasta County, California (ex W. P. Popenoe collection).

Figs. 7–10. *R. (Romaniceras) deverianum* (d'Orbigny). The holotype of *Eucalycoceras constrictum* Spath, 1926 (= *Acanthoceras* aff. *A. newboldi* Kossmat of Pervinqui re, 1911 p. 45, pl. 4, fig. 37). Said to be from Berrouaghia, Algeria (Sorbonne collections).

Figs. 11–16. *Tunesites choffati* Pervinqui re. 11–14 paratype from A. ez Zerga; 15–16 holotype, from Koudiat el Hamra, Tunisia (Sorbonne collections).

Figs. 19–23. *Tunesites salammbo* Pervinqui re. Holotype, from Djebel Guern Halfaya, Tunisia (Sorbonne collections).

Fig. 23. *Houreceras hourqi* Collignon. Inner whorls of a specimen from the late Cenomanian of Ankilimanarivo, Madagascar, in C. W. Wright's collection.



KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

- 1939 *Romaniceras uchauxiense* Collignon, pp. 89, 94, pl. 10, fig. 1, 1a.
 1951 *Romaniceras* sp., Wright and Wright, p. 29 (pars).
 1957 *Romaniceras* aff. *uchauxiense* Collignon; Matsumoto, Saito and Fukada, p. 24, pl. 9, figs. 1a-c, 2; pl. 14, fig. 1a-b; pl. 15, fig. 2.
 1957 *Romaniceras pseudodeverianum* (Jimbo); Matsumoto, Saito and Fukada, p. 22, pl. 8, fig. 3; text-fig. 7a-d.
 ?1957 *Romaniceras* (?) *otatumei* Matsumoto, Saito, and Fukada, p. 25, pl. 2, fig. 2a-b.
 1958 *Acanthoceras sharpei* Zázvorka, p. 43 (pars.), pl. 2, figs. 3-4 (non 5).
 1958 *Acanthoceras deverianum* (d'Orbigny); Zázvorka, pl. 1, figs. 1, 2.
 ?1959 *Romaniceras* aff. *pseudodeverianum* (Jimbo); Matsumoto, p. 92, pl. 27, fig. 1a-b; text-fig. 46.
 1965 *Romaniceras deveriai* d'Orbigny; Collignon, p. 22, pl. 384, fig. 1655.
 1965 *Romaniceras uchauxiense* Collignon; Collignon, p. 22, pl. 384, fig. 1656.
 ?1969 *Romaniceras deverianum* (d'Orbigny); Freund and Raab, p. 6.
 1975 *Romaniceras* sp. aff. *R. deverianum* (d'Orbigny); Matsumoto, p. 117, pl. 14, fig. 1a-c.
 1975 *Romaniceras yezeense* Matsumoto, p. 118, pl. 14, fig. 2; pl. 15, figs. 1a-b; text-figs. 5-6.
 ?1975 *Yubariceras otatumei* (Matsumoto, Saito and Fukada); Matsumoto, p. 144, pl. 21, fig. 1a-c; text-figs. 15-16.

Types. The problems associated with the type material are discussed above (p. 327).

Specimens studied. From Uchaux, Vaucluse: MNHP 6781 (d'Orbigny collection), a syntype; EMP, Fontannes collection, a silicified juvenile 83-4 mm in diameter. MNHP, Peron collection (unregistered), two juveniles, 40 and 80 mm in diameter. MNHP, two partially silicified adults collected by Dr. J. Sornay. FSL 14210 (the holotype of *R. (R.) uchauxiense*), 13695.

An unregistered specimen in the MNHP, labelled Faluns de Touraine, and in a Tuffeau Preservation. From the Tuffeau Jaune of Touraine: casts of two specimens (MNHP, LC) Biet collection, from Nouans (Indre et Loire); SP—an unregistered specimen labelled '*Anmonites*' Craie de Touraine (Z. à *Callianassa archiaci*) St. Georges sur Cher?, M. Heb. [art?] 61-624. LC 417BAC, labelled Beidoze, Les Ranges; ?LC (Reignoux collection), unregistered and unlocalized; ?LC unregistered, Carrière du Riveau, Grand Pressigny; LC unregistered, Montlouis-sur-Loire, La Barre; LC unregistered, Loches (l'Etang). The holotype of *Romaniceras sharpei* (Zázvorka), BMNH C 34596 (= Sharpe 1857, p. 46, pl. 19, fig. 5a-b), from the Middle Chalk of Sussex. BMNH C 34946, from the *Terebratulina lata* Zone Middle Chalk of Amberley, Sussex; WW 22746 from 2 m below the Chalk Rock at Latimer, Buckinghamshire.

From southern India we have seen a fine topotype of *Ammonites medicottianus* Stoliczka from Odium in the collections of the Naturhistorisches Museum, Vienna. We have also examined all the Japanese material listed in the synonymy.

The holotype, and only specimen, of *Eucalycoceras constrictum*, which forms the basis of the description of the earliest stages of the species, is in the collections of the Sorbonne. The specimen was collected by P. Thomas and recorded as coming from the middle of his second zone of the Cenomanian at Berrouaghia. In spite of this apparently exact record, the association listed by Perviniquière (1910, p. 78) indicates more than one horizon, and the specimen is unlike any known Cenomanian ammonite. We know from our own field-work that around Berrouaghia the Turonian also yields limonitic nuclei of ammonites.

EXPLANATION OF PLATE 40

Fig. 1 is $\times 2$; the remainder are $\times 1$.

Figs. 1, 3-5. *R. (Yubariceras) ornatissimum* (Stoliczka). 1, inner whorls of GK H5685, from the *Inoceramus hobetsensis* Zone, Hobetsu area, Kyushu, Japan. 3-5, the holotype of *Yubariceras yubarensis* Matsumoto, Saito, and Fukada, UT MM7620 (= 1-343) from a pebble in the bed of the Pankemoyuparo, near the mouth of the Kancobetsu, Oyubari area, Kyushu, Japan.

Figs. 2, 6. *R. (Obiraceras) ornatum* Matsumoto. Holotype, GK H5689, from the Upper Turonian of Sato-nosawa, Obira area, Hokkaido.



KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

Dimensions	D	Wb	Wh	Wb:Wh	U	Ribs
d'Orbigny's original figures	94.0(100)	44.0(47)	39.0(42)	1.13	29(31)	36/37
Holotype of <i>R. (R.) pseudodeverianum</i> (after Matsumoto <i>et al.</i>)	195.0(100)	—(—)	75.0(38)	—	68.5(35)	32
Holotype of <i>R. (R.) uchauxiense</i>	147.5(100)	58.5(40)	68.5(46)	0.85	39.5(27)	31/32
Holotype of <i>R. (R.) yezeense</i> (after Matsumoto)	218(100)	76.0(35)	95.0(43)	0.8	58.0(26)	37
Lectotype of <i>R. (R.) medicottianum</i> (from the figure)	215(100)	97.45	90(42)	1.1	75(35)	23
EMP, coll. Fontannes	83.4(100)	—(—)	39.0(47)	—	25.0(30)	41/42
	76.7(100)	28.0(37)	36.5(48)	0.78	22.7(30)	41/42
MNHP, coll. Peron (distorted)	64.5(100)	31.0(48)	32.5(50)	0.95	15.0(23)	32

Description. The very earliest stages with constrictions are known only from the imperfectly preserved and distorted holotype of *E. constrictum* Spath (Pl. 39, figs. 7–10). The nucleus up to a diameter of 5.5 mm appears to have been evolute, with a depressed, rounded whorl, lacking ornament, so far as is visible. On the outer whorl beyond a diameter of 5.5 mm the earliest ornament to appear is in the form of low, broad, distant ribs, arising as weak bullae, passing forwards across the flank and weakening on the venter which they cross with a broad convexity accompanied, possibly, by weak intercalated ribs. There are initially neither tubercles nor constrictions, but a relatively large clavate ventrolateral tubercle is present at a position 270° back from the end of the specimen (approximately 10 mm diameter), and two strong, slightly flexed, prorsiradial constrictions are developed in the next 90° (Pl. 39, fig. 9). The collar ribs of the first constriction bear umbilical bullae and a ventral node as the only obvious tubercles (although preservation is poor). Those of the second are stronger and bear strong umbilical bullae projected into the umbilicus, conical inner lateral, bullate inner and outer ventrolateral, and a suggestion of a transverse siphonal tubercle. The remainder of the specimen to a (deformed) diameter of 23 mm develops a markedly octagonal, depressed whorl section, with numerous crowded, feebly flexuous ribs, strongly projected forwards across the ventrolateral shoulder but crossing the venter with only a shallow convexity. There are nine rows of tubercles, as noted above, which become progressively stronger as size increases, the siphonal row initially the weakest, the inner ventrolateral, outer ventrolateral, and siphonal rows markedly bullate.

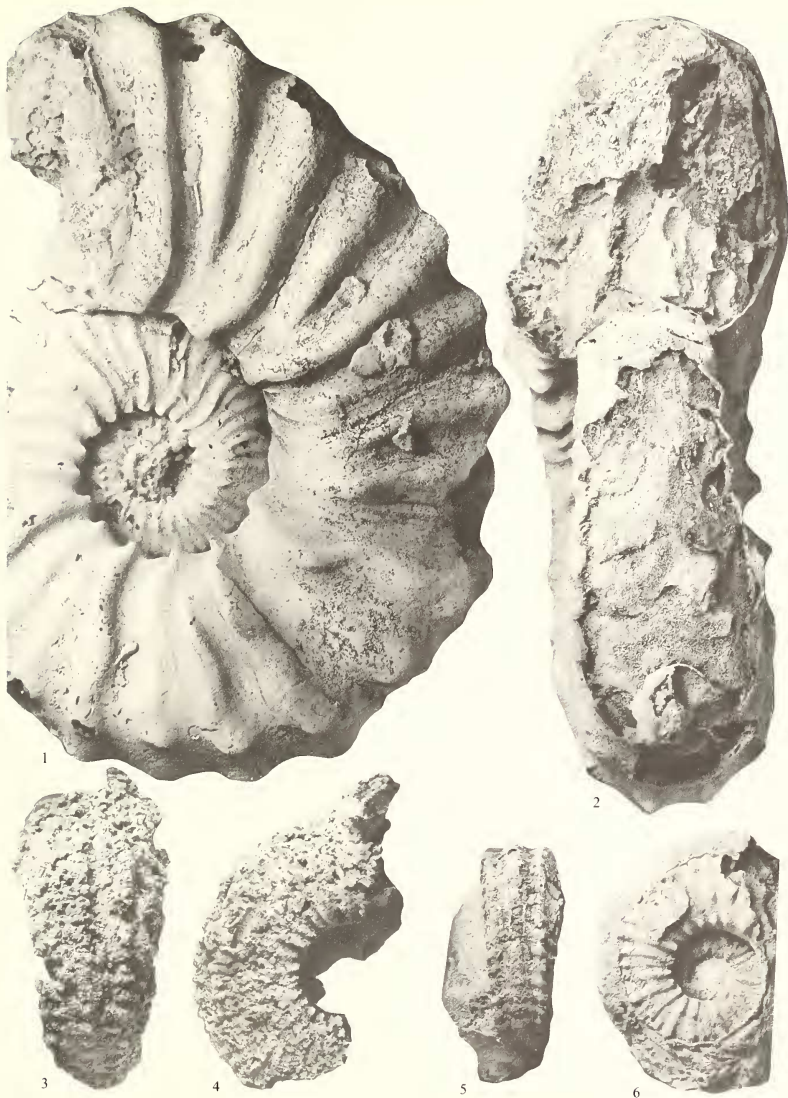
The smallest topotypes before us are 40–50 mm in diameter (Pl. 41, figs. 5, 6) and, like most Uchaux specimens, retain silicified shell. These, like the dorsum of one of the Sornay specimens, show the same style of ribbing and constrictions seen in *E. constrictum*.

Coiling is relatively evolute in middle and later growth, the whorl section varies from slightly depressed to compressed ($Wb:Wh = 0.78–1.13$) and is polygonal, with the greatest breadth at the lateral tubercle. There is a total of 32 to 42 ribs per whorl, the density increasing with whorl-compression. Most ribs arise from umbilical bullae; a few are intercalated low on the flank or extend from the umbilicus without a bulla. Periodically ribs bifurcate from the lateral tubercle. In depressed individuals the ribs are straight and recti- to prorsiradial; in compressed ones they may be gently flexed (Pl. 42, fig. 1). The umbilical bullae project into the umbilicus and in well-preserved individuals become subspinate, resembling in this respect the Cenomanian *E. gothicum* (Kossmat) (1895, p. 69, pl. 25, fig. 3a–c). There are well-developed, more or less bullate, lateral tubercles, conical inner ventrolateral, subequal outer ventrolateral, and siphonal tubercles, rounded on moulds and conical on depressed individuals with shell preserved but all clavate in compressed ones. In these latter the clavi form semi-continuous nodose ridges in some specimens when covered by a dorsal callus (Pl. 42, fig. 2). Well-developed constrictions, parallel to the ribs, are visible on several nuclei up to diameters of at least 30 mm.

As size increases beyond about 70 mm, ribs typically broaden and coarsen and the lateral tubercles may weaken. There is a tendency for long and short ribs to alternate regularly, ribs to become more widely spaced on

EXPLANATION OF PLATE 41

Figs. 1–6. *R. (Romaniceras) deverianum* (d'Orbigny). 1–2, MNHP unregistered (Sornay collection). 3–4, MNHP 6781 (d'Orbigny collection), the surviving syntype. 5–6, MNHP, Peron collection. All specimens are silicified, and from Uchaux, Vaucluse. 1–2 are reduced $\times 0.8$; the remainder are $\times 1$.



KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

the venter and outer ventrolateral and siphonal clavi to elongate markedly. The largest specimens we have seen tend to become high-whorled, and even those with depressed inner whorls and rounded ventral tubercles show this feature (see, e.g., Collignon 1939, pl. 8, fig. 2; pl. 9, fig. 1a).

None of the topotype specimens before us shows the suture line.

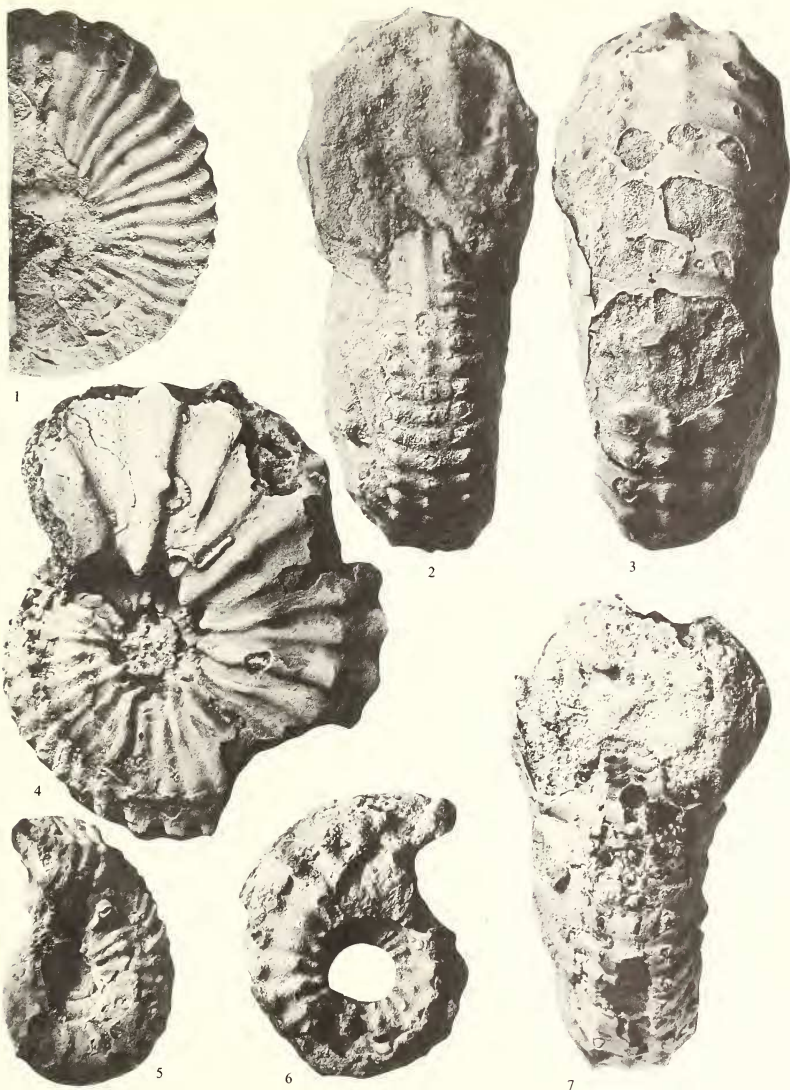
Discussion. The inflated Uchaux specimens, such as the syntype in the d'Orbigny collection and that figured by Roman and Mazeran (1913, pl. 41, fig. 2, 2a), occur with more compressed individuals which develop long, high, *Barroisiceras*-like ventral and siphonal clavi at maturity. Collignon (1939, p. 37) named these *R. uchauxiense*, and subsequent authors have maintained the two species as separate. Both types show the same arrangement of tubercles and both have the characteristic spinate umbilical bulla projecting into the umbilicus. Forms of intermediate inflation are present (Pl. 42, figs. 4, 7). The strongly clavate ventral and siphonal tubercles are a feature of the later growth stages, and even the compressed and densely ribbed individual shown in Pl. 42, figs. 1-3, has the characteristic clavate outer ventrolateral and rounded siphonal tubercles of typical *R. deverianum*. We would also note that the type of *R. uchauxiense* is extreme in its ventral decoration even by comparison with other specimens referred to the species and shows signs of pathological disturbance which have accentuated these features. All the Uchaux specimens share details of ornament and development in common, upon which is expressed a covariance in ribbing style and density linked to a compressed, versus depressed, whorl, as is widely demonstrated in acanthoceratids. In terms of the *Acanthoceras rhotomagense* population described by Kennedy and Hancock (1970), *deverianum* corresponds to *rhotomagense sussexiense* and *uchauxiense* to *rhotomagense clavatum*. The two occur together wherever any numbers of specimens are known, as in Touraine, Japan, and Madagascar, in addition to Uchaux.

Interpreted in this way, a number of other species, we believe, fall into the synonymy of *R. deverianum*. The earliest described of these is *Ammonites medicottianus* Stoliczka (1865, p. 77, pl. 43, fig. 1a-c) from the Uttatur Group north of Odium, southern India. The species is based on several specimens; that illustrated by Stoliczka is here designated the lectotype. We have fortunately been able to study a large topotype in the collections of the Naturhistorisches Museum, Vienna. These specimens show an intermediate degree of inflation and rib density between comparably sized individuals referred by previous authors to *deverianum* and *uchauxiense*, in particular resembling the cast of the larger of the Nouans specimens before us, especially in ventral aspect, but retaining a stronger lateral tubercle. Its inner whorls are relatively finely ribbed compared with the outer, like those of the Madagascan example figured by Collignon (1965, pl. 384, fig. 655); these appear to be differences of individual, rather than specific significance, although we do not know the full range of variation of the Indian population.

R. pseudodeverianum Jimbo (1894, p. 178, pl. 21, fig. 1-1b; see also Matsumoto, Saito and Fukada 1957, p. 22, pl. 8, fig. 3; text-fig. 7A-D) is a Japanese species based on a single specimen (GT. I-106) collected loose in the bed of the Obirashibets River, Teshio Province, Hokkaido; it was made the type species of the subgenus *Proromaniceras* Wiedmann, 1960. All of one side of the type specimen is worn away and previous reconstructions of the whorl section (Matsumoto *et al.* 1957, text-fig. 7A-D) are schematic. Furthermore, almost all of the venter and most of the flank of the outer whorl of the preserved side is waterworn (Pl. 43, figs. 1-3), so that ribs on the last half-whorl are unnaturally weak. The specimen bears bullate umbilical tubercles, strong bullate laterals, and conical to bullate inner ventrolateral tubercles. The outer ventrolateral tubercles are worn but appear to have been strong

EXPLANATION OF PLATE 42

Figs. 1-7. *R. (Romaniceras) deverianum* (d'Orbigny). 1-3, FSL 13965. 4, 7, MNHP, Peron collection. 6, MNHP 1904-32; all specimens silicified, and from Uchaux, Vaucluse. 5, the holotype of *Eucalyoceras constrictum* Spath. See explanation of Plate 1, figs. 7-10 for details. Fig. 5 is $\times 2$; the remainder are $\times 1$.

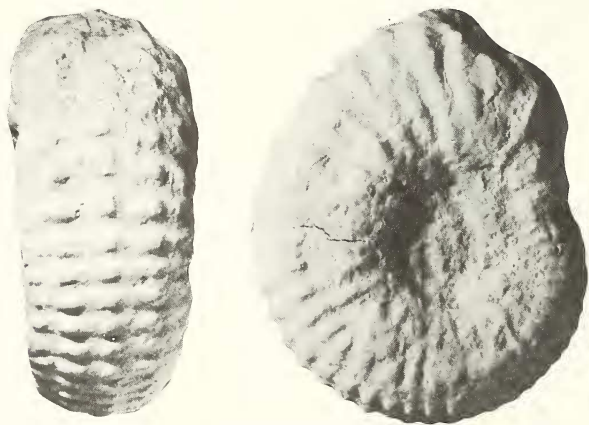


KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

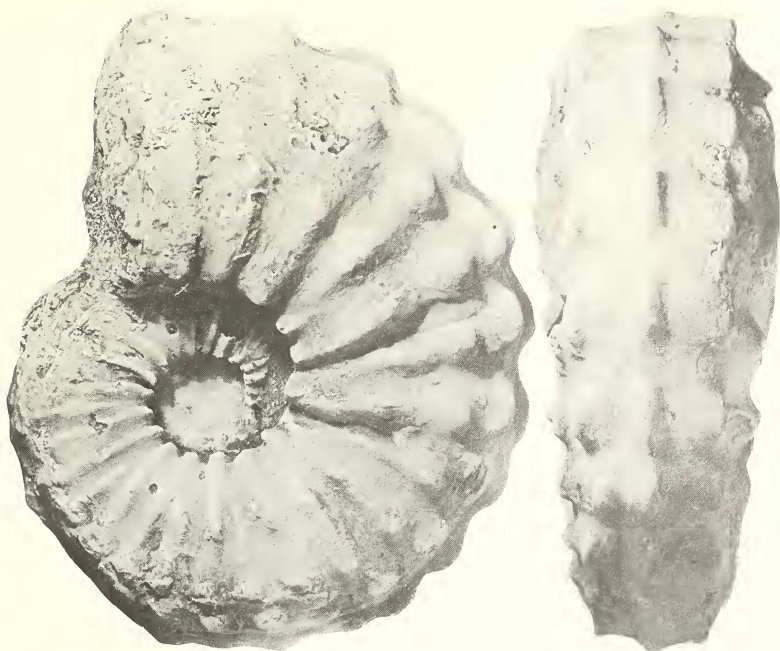
and slightly clavate; the siphonal tubercles are weaker and clavate. There is branching and intercalation of ribs at the smallest diameter visible, but on the last half-whorl most of the ribs are long and are crowded, suggesting that this is a small adult. The type of *R. pseudodeverianum* has the strong ribs of d'Orbigny's protograph, but within the limits of preservation the lateral tubercle appears to remain rather low on the flank throughout growth. As for the ventral tubercles of the last half whorl, both the inner and outer ventrolaterals appear transversely rather than spirally elongate and are in the process of assimilation into a ribbed mature body-chamber ornament. These differences seem to be no more than of individual significance. *Acanthoceras sharpei* Zázvorka (1958, p. 43) was based on Sharpe's specimen (1857, p. 43, pl. 19, fig. 5a-b) of *deverianum*. This (BMNH 34549) has a compressed, flat-sided, whorl section and is more densely ribbed than d'Orbigny's protograph, but corresponds at a similar size to the smaller of the specimens from Nouans (text-fig. 4).

R. kallesi (Zázvorka) (1958, p. 39; text-fig. 1, figs. 1-2) is a distinct, early species of *R. (Romaniceras)* discussed further below. Features which separate it from *R. (R.) deverianum* at a comparable degree of inflation are the rectangular whorl section, lower expansion rate, evolute coiling, and weaker tuberculation, especially in the umbilical bullae; the weak lateral tubercles are low on the flank and are rapidly lost; interspaces are wide on the venter. The species is adult at a much smaller size than *R. deverianum* and none of the specimens of *R. kallesi* before us approach the inflated whorl section and strong lateral tuberculation of typical *deverianum*, nor do they show the compression and clavate ventrolateral tubercles of the slender *uchauxiense* type.

Of the north African forms, *E. constrictum* Spath has already been shown to be based on a juvenile *R. deverianum* (p. 332). *Tunesites choffati* Pervinqui  re (Pl. 39, figs. 11-16) is also a juvenile *R. (Romaniceras)*. The smaller paratype has much stronger ribs on the untuberculate constricted portion and in this respect differs from what we have taken as a *R. deverianum* nucleus (Pl. 39, figs. 7-10); it is specifically indeterminate in our present state of knowledge. The larger holotype is unfortunately crushed but resembles closely the inner whorls of the Uchaux specimen shown as



TEXT-FIG. 4. *R. (Romaniceras) deverianum* (d'Orbigny). Plaster cast of a juvenile specimen (EMP, LC), Biet Collection, from the Tuffeau Jaune de Touraine of Nouans, Indre-et-Loire.



TEXT-FIG. 5. *R. (Romaniceras) deverianum* (d'Orbigny). Plaster cast of the holotype of *R. (Romaniceras) uchauxiense* Collignon, FSL 13964, from Uchaux, Vaucluse. Reduced $\times 0.8$ approx.

Pl. 41, figs. 5–6; it too may thus be a synonym of *R. deverianum*, in spite of the obvious differences from the type of *E. constrictum*.

R. (R.) otatumei Matsumoto, Saito and Fukada (1957, p. 25, pl. 2, fig. 2; Matsumoto 1975, p. 144, pl. 21, fig. 1; text-figs. 15–16) is a further species based on a juvenile which may be within the range of *R. deverianum*, having, however, much stronger lateral tubercles on some ribs. It resembles the type of *T. choffati* at the same size.

Yubariceras japonicum Matsumoto, Saito and Fukada (1957, p. 31, pl. 8, fig. 2; text-figs. 11, 12; Matsumoto 1975, p. 139, pl. 19, figs. 2–3; pl. 21, fig. 2; text-figs. 13–14) has only nine rows of tubercles and is a typical *R. (Romaniceras)*. It appears to be one of those passage forms of intermediate inflation that compares with the Uchaux specimen shown in Pl. 42, fig. 2, even to the point of having the same dorsal callosity.

'*Yubariceras*' aff. *japonicum* of Matsumoto (1975, p. 143, pl. 21, figs. 3–4; pl. 23, fig. 2) has parallel flanks, a rounded venter, distantly spaced, low, flexuous, prorsiradial ribs and bullate lateral tubercles quite close to the umbilical; it is quite distinct from any European specimen we have seen.

'Y.' *pseudomphalum* Matsumoto (1975, p. 146, pl. 22, fig. 1) is based on a single specimen from the Oyubari area of Hokkaido. It has nine rows of tubercles but differs from *R. deverianum* in its depressed whorl section and primary ribs, differentiated into relatively weak and relatively strong with intercalated ventral ribs on the phragmocone but all the body-chamber ribs long. This *Euomphaloceras*-like form is quite distinctive.

'Y.' *fujishimai* Matsumoto (1975, p. 148, pl. 22, fig. 2; pl. 23, fig. 3; text-fig. 17) has nine rows of tubercles and is also based on a single specimen from the Oyubari area of Hokkaido. Like *R. pseudomphalum* (from which it may not be specifically separate) it has intercalated *Euomphaloceras*-like ventral ribs and tubercles which immediately distinguish it from *R. deverianum*.

The *Romaniceras* described from Mexico by Jones (1938) are in part *Shuparoceras* (e.g. *R. indiduraense* Jones, p. 119, pl. 7, figs. 2-4; and perhaps '*Romaniceras*' *santaanaense* Jones, p. 121, pl. 8, figs. 1, 6). *Romaniceras kanei* Jones (1938, p. 120) is a *R. (Yubariceras)*. The types of *R. adkinsi* Jones (1938, p. 120, pl. 8, figs. 4, 5) and *R. mexicanum* Jones (1938, p. 121, pl. 7, figs. 1, 6) are so poor that the species should be treated as *nomina dubia*. They differ from *R. deverianum* in having massive whorls with broad, flattened venters. *R. (?) coahuilaense* Jones (1938, p. 118, pl. 6, fig. 1; pl. 8, fig. 5), which may be similarly separated, is coarsely and grossly ribbed and tuberculate. *R. toribioense* Jones (1938, p. 122, pl. 7, figs. 7-8) is based on a very poor fragment and although it might be a part of a slender *R. deverianum* is best treated as generically indeterminate. The *R. uchauxiense* of Reymont (1955, p. 46, pl. 9, fig. 2) shows doubling of the ventral tubercles and appears to be a fragment of an *Obriceras*.

Occurrence. *R. (R.) deverianum* is a late mid Turonian species known from southern England, Touraine and Vauluse in France, Bohemia, Algeria, Tunisia (?), Israel (?), Madagascar, southern India, and Japan.

Romaniceras (Romaniceras) kalesi (Zázvorka, 1958)

Pl. 44, figs. 1-3; Pl. 45, figs. 2-7; Pl. 46, figs. 1-4; Pl. 47, figs. 1-4; text-fig. 6

1958 *Acanthoceras kalesi* Zázvorka, p. 39, pl. 1, figs. 1-2.

1958 *Acanthoceras*, Zázvorka pl. 2, fig. 5 only.

1960 *Romaniceras (Proromaniceras) pseudodeverianum hispanicum* Wiedmann, p. 735, pl. 2, figs. 3, 4.

1964 *Romaniceras (Proromaniceras) pseudodeverianum hispanicum* Wiedmann, p. 123, text-fig. 4a-b.

1977 *Romaniceras hispanicum* Wiedmann; Hancock, Kennedy, and Wright, pp. 156 et seq.

Types. The holotype is the original of Zázvorka 1958, pl. 1, fig. 1, no. 36938, and the paratype no. 2119, the original of his pl. 1, fig. 2, both from the Turonian Spongolith facies of the White Mountain near Prague, Czechoslovakia.

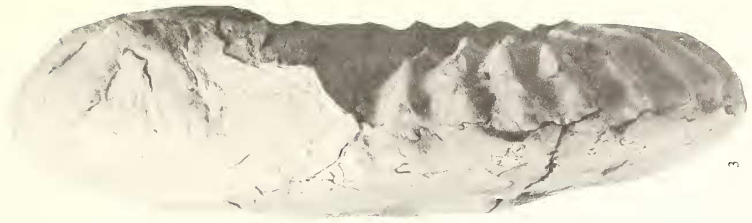
Material studied. Casts and photographs of the holotype of *Romaniceras kalesi*, supplied through the courtesy of Drs. R. Zázvorka and V. Houša, plus a cast of a topotype in the British Museum (Natural History) no. 88992.

Specimens in the Muséum d'Histoire Naturelle, Angers, are: AM 18, 34a-b, 35, from St Cyr-en-Bourg; AM 47, from Saumoussay; AM 45, 114, 115, from Saumur; AM 33 from Montsoreau, and AM 119-120 from Chateaufort-sur-Loire. A fine unregistered specimen in the collections at Nantes is simply labelled 'Touraine'. OUM KZ755-757 collected by us from the St Cyr-en-Bourg Fossil Bed, Champignonnière Les Rochains, 7 km south of Saumur and north-east of Montreuil-Bellay, Maine et Loire.

Through the courtesy of Professor Dr. J. Wiedmann (Tübingen) we have also been able to study a cast of the holotype of *R. (R.) hispanicum*.

EXPLANATION OF PLATE 43

Figs. 1-3. *R. (Romaniceras) deverianum* (d'Orbigny). The holotype of *Acanthoceras pseudodeverianum* Jimbo, the type species of *Proromaniceras* Wiedmann, 1960. This badly worn specimen, GT 1-106 (= MM7516) is from a boulder in the bed of the Opirashibets, Teshio Province, Hokkaido, Japan. Reduced $\times 0.7$.



KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

<i>Dimensions</i>	<i>D</i>	<i>Wb</i>	<i>Wh</i>	<i>Wb: Wh</i>	<i>U</i>	<i>R</i>
Nantes specimen	141.0(100)	48.5(34)	54.5(39)	0.9	53.0(38)	43
AM 114	97.5(100)	40.0(41)	39.0(40)	1.0	33.0(34)	41
AM 34a	146.0(100)	53.0(36)	54.0(37)	0.98	52.0(36)	35
AM 35	114.0(100)	47.0(41)	50.0(44)	0.94	37.0(32)	—

Description. This is a rather small species, adult at 100–150 mm. Coiling is evolute, with a moderately deep umbilicus which comprises 32–38% the diameter. The umbilical wall is rounded and undercut; the whorl section quadrate, with parallel sides, flattened shoulders, and a broad flattened venter. The greatest breadth is at the lateral tubercle and the whorl breadth to height ratio varies between 0.9 and 1.0. Ornament consists of 35–43 narrow, distant, rather delicate ribs per whorl. These arise at the umbilical seam and are low swellings across the umbilical wall. They usually strengthen at the shoulder into weak bullae and become wider and higher on the outer flank, which they cross in a rectiradial to gently prorsiradial direction. There is some variation in strength; in robust forms the ribs are straight, whereas in slender individuals they may be flexed. Most of the ribs are long and arise singly from bullae, but in some specimens they are untuberculate, passing the umbilical shoulder as mere striae, or rarely springing in pairs from a bulla. Occasional shorter, intercalated ribs, arising low or high on the flank, are also present. There are nine rows of tubercles; weak umbilical bullae; bullate laterals; stronger, conical inner ventrolaterals; strong feebly clavate or bullate outer ventrolaterals; and a weak siphonal set. On the venter the ribs commonly weaken between the outer ventrolateral and siphonal rows.

On bodychambers the ribs become markedly convex towards the adult aperture, the lateral and inner ventrolateral tubercles may weaken markedly, but the outer ventrolateral rows survive undiminished.

The sutures are poorly exposed in all our specimens but include a deep E, broad bifid E/L, narrow L, and relatively large, bifid L/U₂.

Discussion. Zázvorka's figures are side views only but show a densely and finely ribbed form which matches closely the Touraine material before us, as confirmed by casts of the holotype (text-fig. 6) and a Czech topotype (Pl. 45, figs. 3–4). These in turn are closely comparable with the poorly preserved holotype of *R. (R.) hispanicum* Wiedmann (= *R. (Proromaniceras) pseudodeverianum hispanicum* of Wiedmann 1960, 1964), which we take to be a synonym (Pl. 45, figs. 5–7). What appears to be the early developmental stages of this species are represented by a beautiful specimen from the Mancos Shale at USGS Mesozoic Locality 15925, in the southern part of the San Juan Basin, New Mexico (Pl. 45, fig. 2). At 17.5-mm diameter it shows a typical *Tunesites*-like stage, with deep, narrow, convex prorsiradial constrictions flanked by narrow, rounded ribs bearing umbilical, ventrolateral, and siphonal tubercles, preceding a densely ribbed rectangular-whorled stage with nine rows of tubercles. The early development of *R. kallesi* is thus similar to that of *R. deverianum* (so far as this is visible in our specimens—cf. Pl. 39, figs. 7–10). In middle and later growth the two can be distinguished on the following criteria: *R. kallesi* is a small species; at a comparable degree of inflation it is delicately and narrowly ribbed; it has ribs that are dominant over weaker tuberculation; on the venter the ribs are narrower and more widely spaced and there is a tendency for the venter and flanks to remain flattened rather than becoming convex. It never develops the strongly clavate ventral and siphonal nodes of compressed (*uchauxiense*) individuals.

Two Touraine specimens, best referred to as *R. aff. kallesi*, show interesting features which point, even in this, the earliest species, to the origins of *R. (Yubariceras)* and *R. (Obiraceras)*. AM 46 (Pl. 47, figs. 1–2), labelled '*Acanthoceras ornatisimum* Stoliczka, Saumoussay (M et L), Collection Valontaire', is a mature specimen with the following dimensions: D = 115.0(100); Wb = 50.0(43); Wh = 45.0(39); U = 36.5(32); Wb: Wh = 1.11; R = 36. It is septate to a diameter of approximately 70 mm, and on this portion the ribs are of unequal strength and length, those arising at the umbilicus

EXPLANATION OF PLATE 44

Figs. 1–3. *R. (Romaniceras) kallesi* Zázvorka. Adult specimen from Touraine in collections of the Museum d'Histoire Naturelle, Nantes.



3



2



1

KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

having relatively strong bullae. All ribs bear weak inner and stronger outer lateral bullae, together with strong inner and outer ventrolateral and siphonal tubercles. On the body chamber the outer lateral tubercles have disappeared and the inner lateral are weak, leaving a total of only nine rows, while there are many more intercalated ribs. The over-all style and proportions link this specimen to *R. kalesi* but the eleven rows of tubercles of the phragmocone suggest affinities with *R. (Yubariceras)*; we would suggest that this may indeed be an intermediate in which *R. (Yubariceras)* features are developed only briefly and not retained to maturity.

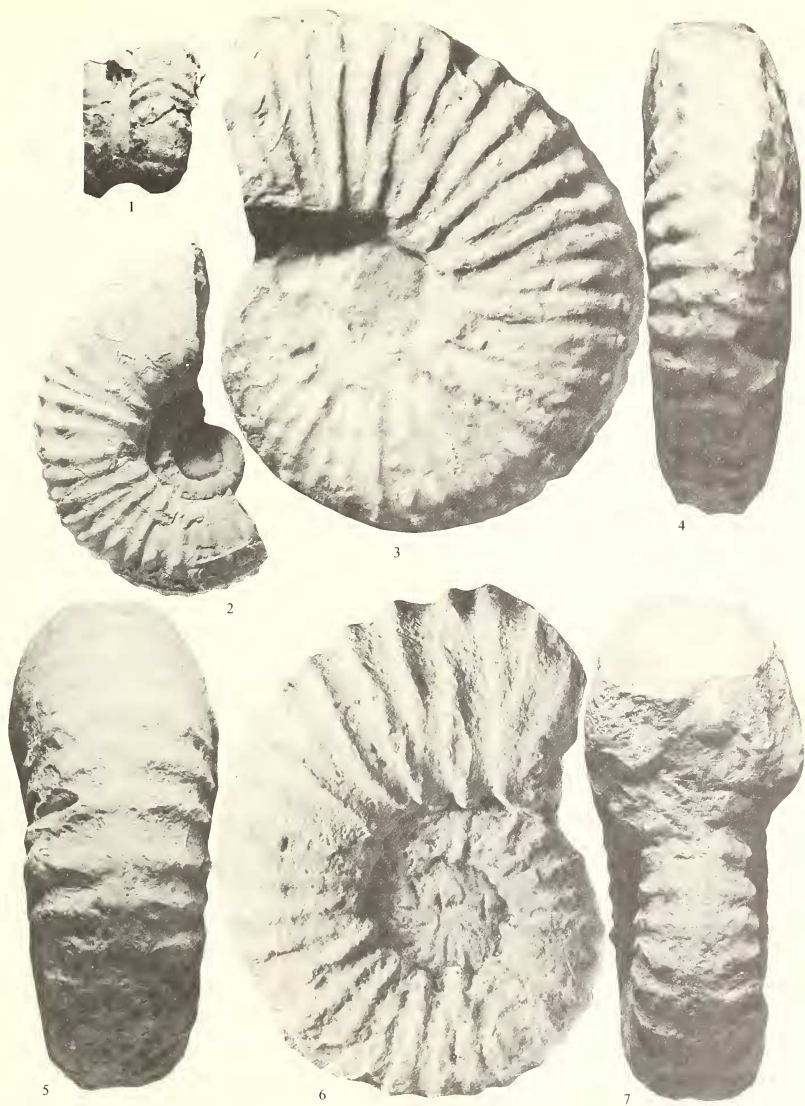


TEXT-FIG. 6. *R. (Romaniceras) kalesi* Zázvorka. Plaster cast of the holotype, no. 36938, from the Turonian Spongolith facies of the White Mountain, near Prague.

EXPLANATION OF PLATE 45

Fig. 1. *R. (Yubariceras) ornatissimum* (Stoliczka). Ventral view of an unregistered MNHP specimen (de Grossouvre collection), showing constrictions.

Figs. 2-7. *R. (Romaniceras) kalesi* (Zázvorka). 2 is a cast of a specimen from the Mancos Shale, *Prionocyclus hyatti* Zone, at USGS Mesozoic Locality 15925, San Juan Basin, New Mexico. The original is in the U.S. Geological Survey Collections, Denver. 3-4 are of BMNH 88992, a cast of a specimen from the Weisserberg, Czechoslovakia. 5-7 are of casts of the holotype of *Romaniceras (Proromaniceras) hispanicum* Wiedmann, the original is from an unknown horizon near Ciudad, Burgos, Spain, and is in the Ciry collection, housed in the Institut de Géologie, Université Dijon.



KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

The second specimen, AM 33 (Pl. 47, figs. 3-4), also labelled '*Acanthoceras ornatissimum* Stoliczka', is from Montsoreau (Maine et Loire). Although clearly of the *kallesi* group, it shows an incipient doubling of the outer ventrolateral tubercles (more readily felt than photographed—Pl. 47, fig. 3), suggesting affinity with *R. (Obiraceras)* in which both inner and outer ventrolateral tubercles have this feature.

Occurrence. Early mid Turonian of western Czechoslovakia; Touraine, France; Burgos, Spain; and possibly New Mexico, U.S.A.

Subgenus *Yubariceras* Matsumoto, Saito, and Fukada, 1957

Romaniceras (Yubariceras) ornatissimum (Stoliczka)

Pl. 39, figs. 1-6; Pl. 40, figs. 1, 3-5; Pl. 45, fig. 1; Pl. 48, figs. 1-4; Pl. 49, figs. 1-8; Pl. 50, figs. 1-4; text-figs. 3E, 7, 8

- 1863 *Ammonites deverianus* d'Orbigny; Pictet, p. 36, pl. 7.
 1865 *Ammonites ornatissimus* Stoliczka, p. 75, pl. 40.
 1889 *Ammonites deverioides* de Grossouvre, p. 524, pl. 12, figs. 1, 2 (including varieties *inermis* and *armata*).
 1896 *Ammonites deverioides* de Grossouvre; Peron, p. 21, pl. 1, figs. 2-3.
 1897 *Acanthoceras ornatissimum* Stoliczka; Kossmat, p. 16.
 1901 *Acanthoceras Bizeti* de Grossouvre, p. 780.
 ?1924 *Acanthoceras Shastense* Reagan, p. 242, pl. 20, figs. 1, 2; pl. 60, fig. 5.
 1931 *Romaniceras cummingsi* Adkins, p. 43, pl. 3, fig. 6.
 1931 *Romaniceras loboense* Adkins, p. 44, pl. 2, figs. 1, 21; pl. 3, fig. 5.
 1937 *Acanthoceras deverianum* d'Orbigny; Basse, p. 180, pl. 8, figs. 1a-h, 2a-b.
 1939 *Romaniceras deverioides* de Grossouvre; Collignon, pp. 90 et seq.
 1939 *Romaniceras ornatissimum* Stoliczka; Collignon, pp. 90 et seq.
 1947 *Acanthoceras ornatissimum* Stoliczka; Lecointre, pl. 2, fig. 6.
 non 1955 *Romaniceras* aff. *deverioides* (de Grossouvre); Reymont, p. 46, pl. 9, fig. 1a-b; text-figs. 18b, 19.
 1957 *Yubariceras yubarensis* (ex Yabe MS.) Matsumoto, Saito and Fukada, p. 27, pl. 8, fig. 1; pl. 10, fig. 1; pl. 11, fig. 1; pl. 13, fig. 1; pl. 15, fig. 1; text-figs. 8-9.
 ?1958 *Acanthoceras shastense* Reagan; Anderson, p. 242, pl. 20, figs. 1-2; pl. 60, fig. 5.
 1958 *Mantelliceras conquistador* Anderson, p. 245, pl. 15, fig. 2.
 1958 *Romaniceras hesperium* Anderson, p. 246, pl. 23, fig. 1, 1a.
 ?1959 *Eucalycoceras* (?) *shastense* (Reagan); Matsumoto, p. 94, pl. 23, fig. 1a-c; pl. 24, figs. 2a-b, 3a-b; text-figs. 47-49.
 1959 *Romaniceras deverioides* (de Grossouvre); Matsumoto, p. 87, pl. 25, fig. 1a-c; pl. 26, fig. 1a-c; pl. 28, fig. 1a-b; pl. 29, fig. 4a-c; text-figs. 40-44.
 1965 *Yubariceras yubarensis* Matsumoto; Collignon, p. 24, pl. 385, fig. 1657.
 1969 *Romaniceras deverioides* (de Grossouvre); Freund and Raab, p. 7.
 1975 *Romaniceras deverioides* (de Grossouvre); Matsumoto, p. 121, pl. 15, fig. 2a-b; text-fig. 7.
 ?1975 *Romaniceras* [New Genus?] *aequicostatum* Matsumoto, p. 124, pl. 15, fig. 3a-b; text-fig. 8.
 1975 *Yubariceras yubarensis* Matsumoto, Saito and Fukada; Matsumoto, p. 133, pl. 19, fig. 1a-b; text-fig. 11.
 1975 *Yubariceras* sp. aff. *Y. ornatissimum* (Stoliczka); Matsumoto, p. 135, pl. 17, fig. 2; pl. 18, fig. 1.
 1975 *Yubariceras ornatissimum* (Stoliczka); Matsumoto, text-fig. 12.

EXPLANATION OF PLATE 46

Figs. 1-4. *R. (Romaniceras) kallesi* (Zázvorka). 1-2, AM 47, from Saumoussay, Maine-et-Loire. 3-4, AM 45, from Saumur, Maine-et-Loire.



1



2



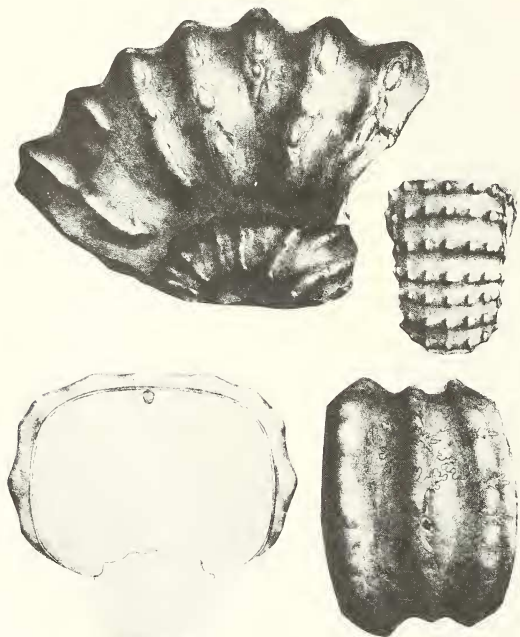
3



4

Type. The holotype, by monotypy, is the original of Stoliczka's (1865), p. 75, pl. 40, fig. 1a-e. This specimen is preserved in the collections of the Indian Geological Survey at Calcutta, no. 174, and is from the Uttatur Group at Odium, southern India (see text-fig. 7).

Other material studied. We have seen over thirty specimens, mostly from either Bourré (Loire-et-Cher) or Poncé (Sarthe), and there is material in most of the large French and British collections. From Bourré: the lectotype of *R. deverioides* (= de Grossouvre 1889, pl. 12, figs. 1-2) in the collections of the Ecole des Mines; MNHP 1896-27, de Vibraye collection; MNHP (unregistered) a 50-mm nucleus and part of a strongly tuberculate outer whorl. Numerous unregistered specimens: EMP, MNHP, SP, FSM, FSR. BMNH 34593, 37689, and C74804: FSM 13.962.



TEXT-FIG. 7. *R. (Yubariceras) ornatissimum* (Stoliczka); copy of Stoliczka's (1865). Figures of the holotype. Reduced $\times 0.5$ approx.

EXPLANATION OF PLATE 47

Figs. 1-4. *R. (Romaniceras) aff. kallesi* (Zázvorka). 1-2, AM 46, from Saumoussay, Maine-et-Loire, with eleven rows of tubercles on the phragmocone, suggesting affinities with *R. (Yubariceras)*. 3-4, AM 33, from Montsoreau, Maine-et-Loire, with incipient doubling of outer ventrolateral tubercles, suggesting affinities with *R. (Obiraceras)*.



1



2



3



4

From Poncé: EMP A301, 'Collection Laville, June 15, 1897'; MNHP 6781a (d'Orbigny collection), four individuals, including that figured by Basse (1937, pl. 8, fig. 2a-b) as a 'co-type' of *R. deverianum*; MNHP, 3 unregistered specimens labelled 'Environs de Poncé, Rive dr. du Cher (Sarthe)' and 'Carrières de Ruille'; MNHP 1896-27, 170 mm in diameter; MNHP unregistered, a 165-mm long fragment. MNHP 1895-9, collection Durand; MNHP unregistered, but labelled '*R. ornatissimum*, Ligerian sup. Poncé, Sarthe'. BMNH C2798; FSL 13. 96.3. Numerous unregistered specimens: EMP, MNHP, SP, FSM, FSR.

From Montrichard (Loir et Cher) MNHP 6781b (d'Orbigny collection). From Tourtenay (Deux Sevres): FSL 13966 'Touraine'; MNHP 6781c (d'Orbigny collection).



TEXT-FIG. 8. *R. (Yubericeras) ornatissimum* (Stoliczka). Adult bodychamber in the collections of the Faculté des Sciences, Le Mans, from Poncé, Sarthe. Reduced $\times 0.45$.

EXPLANATION OF PLATE 48

Figs. 1-4. *R. (Yubericeras) ornatissimum* (Stoliczka). 1-2, the lectotype of *Ammonites deverioides* de Grossouvre, from Bourré, Loir-et-Cher. 3-4, MNHP 6781a (d'Orbigny collection) from Poncé, Sarthe, figured by Basse (1937, pl. 8, fig. 2a-b) as a 'co-type' of *Romaniceras deverianum*.



KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

Extra-European specimens include the following: OUMKT 993-996 (ex W. Popenoe collection) from the Bed of Swede Creek, in the Redding area of Shasta County, California; the types of *R. cumminsi* Adkins and *R. loboense* Adkins (Memorial Museum, Austin, Texas); and the types and other specimens of the following Japanese species (details in Matsumoto 1975): *Y. yubarensis* Matsumoto, Saito and Fukada, *R. deverioide* of Matsumoto 1975; *R. aequicostatum* Matsumoto and *Yubariceras* aff. *Y. ornatissimum* Stoliczka.

Dimensions

	D	Wb	Wh	Wb:Wh	U	Ribs
Lectotype of <i>R. deverioide</i>	122.5(100)	62.0(51)	51.8(42)	1.19	38.3(31)	26/27
EMP;	at 98.2(100)	52.5(53)	43.0(44)	1.22	30.0(31)	26/27
MNHP 6781b (d'Orbigny coll.)	at 100 (100)	47.0(47)	41.0(41)	1.15	31.8(31.8)	27/28
MNHP 1896-27 (coll. Vibraye)	135.0(100)	61.6(46)	55.0(41)	1.12	44.5(33)	—
MNHP 6781 (d'Orbigny coll.)	150.0(100)	61.5(41)	57.0(38)	1.1	53.5(36)	32/33
MNHP 6781a (d'Orbigny coll.)	51.7(100)	22.7(44)	21.1(41)	1.1	— (—)	—
MNHP unregistered	a 73.5(100)	40.3(55)	32.5(44)	1.24	— (—)	24/25
Poncé, Carr. de Ruillé	at b 61.0(100)	31.7(52)	26.4(43)	1.2	— (—)	—
MNHP 6781a (coll. d'Orb.)	at 120.0(100)	51.5(43)	37.5(31)	1.37	— (—)	30/31
MNHP 1896-27	at 143.0(100)	78.0(55)	63.5(44)	1.23	43.2(30)	26
MNHP	c 145.0(100)	90.0(62)	62.0(43)	1.45	45.8(32)	25/26
Liger Sup.	ic 145.0(100)	76.0(52)	57.0(39)	1.33	45.8(32)	25/26
Poncé	c 120.0(100)	68.0(57)	53.0(44)	1.28	38.0(32)	26/27

Description. The smallest individual we have seen is a nucleus extracted from a Californian example kindly sent by Professor W. Popenoe; illustrated as Pl. 39, figs. 1-6, it shows a typically constricted '*Tunesites*' nucleus; this can also be seen in our photograph (Pl. 40, fig. 1) of the specimen GK.H5685 figured by Matsumoto (1975, pl. 15, fig. 2a-b). These link with the smallest Touraine specimens, illustrated as Pl. 45, fig. 1, Pl. 48, figs. 3-4, and Pl. 49, figs. 1-4, which vary from rather slender to depressed individuals, which are evolute, with an umbilicus of moderate depth and a rounded to reniform intercostal section with a broadly rounded venter.

There is great variation in rib density, from 25 to 35 per whorl. In some individuals the ribs are straight and recti- to prorsiradiate, mostly extending to the umbilicus with weak to strong umbilical bullae (Pl. 49, figs. 1-2). There may be branching of ribs from bullae (Pl. 49, figs. 3-4), whilst intercalated ribs are very variably developed, sometimes arising low on the flank (Pl. 49, fig. 3), sometimes not starting until just below the shoulder. There are a total of eleven rows of tubercles: umbilical, lateral, inner and outer ventrolateral, ventral, and siphonal.

Umbilical tubercles are commonly bullate; laterals vary from bullate to rounded/conical, the remainder may be rounded to clavate. There is wide variation in relative strength and spacing of tubercles, although the lateral tubercle is often strong. Constrictions are prominent but sparse (up to 5?) on all juveniles, occurring up to 50 mm diameter. They parallel the ribs and are most strongly developed across the venter.

In middle and later growth, it is convenient to describe the specimens under three groups:

Form A (= *R. deverioide* de Grossouvre) (Pl. 48, figs. 1-2; Pl. 49, fig. 8)

The whorl section is depressed, with a whorl breadth to height ratio of around 1.2, with a relatively low whorl expansion rate. Ribs alternate regularly long and short, the long ribs bearing a full complement of eleven rows of tubercles; short ribs bear only seven.

Form B (typical *ornatissimum*) (Pl. 50, figs. 3-4)

An inflated form, with very broad, flattened venter and a reniform, very depressed whorl section. The lateral tubercle tends to be lengthened into a spine in some individuals.

Forms A and B reach a massive size (up to 500 mm) and are connected by gradations at all sizes.

EXPLANATION OF PLATE 49

Figs. 1-8. *R. (Yubariceras) ornatissimum* (Stoliczka). 1-2, MNHP 6581 (d'Orbigny collection), Poncé, Sarthe. 3-4, MNHP, de Grossouvre collection, Poncé, Sarthe. 5-7 is a square-whorled specimen from Touraine close to the holotype of *Yubariceras yubarensis* illustrated in Plate 40, figs. 3-5. 8, ventral view of the lectotype of *Ammonites deverioide*; see explanation of Plate 48 for details.



KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

Form C (inermis de Grossouvre) (Pl. 50, figs. 1-2)

A slender, slowly expanding form; tubercles are subsidiary to ribs and may disappear altogether at diameters of 100 mm upwards. Juveniles are connected by gradations to Form B above; adults are distinct.

We believe that A and B are probably macroconchs and C are microconchs.

The suture line (text-fig. 3E) is of basic *Acanthoceras* type, with broad bifid saddles and narrower lobes.

Discussion. The Touraine populations of *R. (Y.) ornatissimum* show very wide variation, although all pass through smooth serpentine constricted ribbed and multituberculate stages during early growth. In middle growth there is great variation in inflation and relative strength of tubercles and ribs, as well as relative development and spacing of tubercles. Onset of adult features—chiefly loss of tubercles and dominance of ribs—occurs at disparate sizes; we have some individuals adult at 120 mm and others which approach 500 mm. These suggest that there may be an as yet unconfirmed dimorphism in the group, although it must be admitted that most specimens are either large phragmocones or adults and that small adults are rare.

This range of variation is not unusual in acanthoceratids (e.g. Kennedy and Hancock 1970; Juignet and Kennedy 1977) and we are confident that but a single species is present, as is shown by the continuous variation in our series. De Grossouvre (1889) was well aware of this variation and used three names for his material, *deverioides* and vars. *inermis* (renamed *Acanthoceras bizeti* in 1901, p. 780) and *armata*.

Although a lectotype of *R. deverioides* has been designated (Matsumoto 1959, p. 87), there are no specimens which can be proved to be those which de Grossouvre had in mind when creating his varieties. It is, however, clear that he studied the many *Romaniceras* from localities such as Loches, Bourré and Poncé, including those in the École des Mines, Muséum d'Histoire Naturelle and Sorbonne, amongst other museums. In order to provide an objective basis for discussion we would therefore designate as lectotype of *Acanthoceras deverioides inermis* the fine specimen in the School of Mines illustrated as Pl. 50, figs. 1-2, EMP A301, Laville coll., from Poncé. As lectotype of *A. deverioides armatum*, we designate the Poncé specimen in the Muséum d'Histoire Naturelle illustrated as Pl. 50, figs. 3-4.

Subsequent interpretations of *R. deverioides* have varied greatly, but there have been two main schools. Kossmat, the first revising author, concluded that *R. (Y.) deverioides* was a strict synonym of *R. (Y.) ornatissimum* (Stoliczka) (Kossmat 1898, p. 132, text-figs. 2-4) on the basis of the comparable whorl section of Stoliczka's type and a specimen from Ruillé (Sarthe). This view was also taken by Diener (1925) and Zázvorka (1958).

In contrast, Collignon (1939, p. 37) retained *deverioides* and *ornatissimum* as separate species on the grounds that in the former the whorl section is higher than wide, the ribs are straight, and the tubercles are sharp instead of round and blunt. Perhaps the clearest statement on the forms of *R. (Y.) deverioides* comes from Matsumoto (1959) who thought *R. deverioides* specifically distinct from *R. ornatissimum*, of which he regarded *R. deverioides armatum* a synonym, with *R. inermis* as a further separate species.

In 1975 Matsumoto placed *deverioides* and *ornatissimum* in different genera, referring the former to *Romaniceras* and the latter to *Yubariceras*.

The Sarthe populations before us include medium-sized individuals, in particular those which have been referred to as *R. (Y.) deverioides armatum*, which match in all respects the holotype of *ornatissimum*. Furthermore, these intergrade with *R. (Y.) deverioides deverioides* and we see no basis for separating these forms. *R. deverioides inermis* is also no more than a variant or perhaps dimorph. We retain none of these as separate species.

EXPLANATION OF PLATE 50

Figs. 1-2. *R. (Yubariceras) ornatissimum* (Stoliczka). Lectotype of *Ammonites deverioides* var. *inermis* de Grossouvre, EMP A301, Laville Collection, Poncé, Sarthe. Reduced $\times 0.6$ approximately.

Figs. 3-4. *R. (Yubariceras) ornatissimum* (Stoliczka). MNHP 1826-27, from Poncé, Sarthe, the lectotype of *Ammonites deverioides armatum* de Grossouvre. Reduced $\times 0.6$ approximately.



KENNEDY, WRIGHT and HANCOCK, *Romaniceras*

Yubariceras yubarens (Matsumoto, Saito and Fukada) (1957, p. 27, pl. 8, fig. 1; pl. 10, fig. 1; pl. 11, fig. 1; pl. 13, fig. 1; pl. 15, fig. 1; text-figs. 8-9; Matsumoto 1975, p. 133, pl. 19, fig. 1; text-fig. 11) is based on a series of specimens from Hokkaido; the holotype is refigured here as Pl. 40, figs. 3-5. Matsumoto (1975, p. 135) separated *R. (Y.) yubarens* from *R. (Y.) deverioides* in that the former had a square-whorled, *Acanthoceras*-like shell form and the latter a round-whorled *Calycoceras*-like shell form, and that constrictions extended to middle growth in *Y. yubarens* and were in general better marked. As can be seen from Pl. 45, fig. 1, the constrictions of the Touraine material are as strong as those of the Japanese, whilst several Touraine specimens have similarly quadrate whorls (e.g. Pl. 49, figs. 5-7). Matsumoto (1975, p. 135) distinguished *Y. yubarens* from *Y. ornatissimum* in that the ribs of the former were weaker, and inner lateral tubercles not so distinct. Again, these are differences between individuals only. So far as can be seen the only specific criterion remaining is the quadrate whorl of *Y. yubarens*, which occurs in some of the European *R. ornatissimum*. The juvenile figured by Matsumoto (1975, pl. 19, fig. 1) is relatively round whorled, so that even this distinction may not be invariable. We do not, therefore, consider that *Y. yubarens* can be maintained as either a separate species or subspecies, although it is possible that the mean of the Japanese population may differ somewhat from that of Touraine.

R. aequicostatum Matsumoto (1975, p. 124, pl. 15, fig. 3, text-fig. 8) is based on a unique specimen from the Turonian of a tributary of the Ikushumbets, Hokkaido; its precise horizon is unknown. It was characterized by (1) small size (68 mm), (2) depressed whorl (-wb:wh ratio is 1.4-1.5), (3) distant strong, long ribs without intercalatories, and (4) eleven rows of tubercles, the ventral three clavate, ventrolaterals sharply pointed, upper laterals smaller, lower laterals prominent, and umbilicals small but distinct (Matsumoto 1975, p. 124).

The holotype is in fact badly deformed and incompletely visible; it can be matched in our Touraine juveniles in many respects, except for its greater depression and absence of secondary ribs. Whorl section may be of no more than intraspecific significance and certain larger specimens have very depressed whorls, whilst some Touraine specimens (e.g. Pl. 48, fig. 4) have predominantly, but not exclusively, long ribs. In the absence of better material we can only take the view that it is probably a juvenile *R. ornatissimum*.

R. (Y.) kanei Jones (1938, p. 120, pl. 8, figs. 2, 7, 8; pl. 9, fig. 6; see also Matsumoto 1975, p. 123, pl. 19, fig. 4) is based on a single specimen from an unknown locality and horizon in Coahuila, Mexico, refigured here as text-fig. 9. It is readily separable from *R. ornatissimum* by its evolute, almost serpenticone, coiling and slowly expanding, polygonal whorl section.

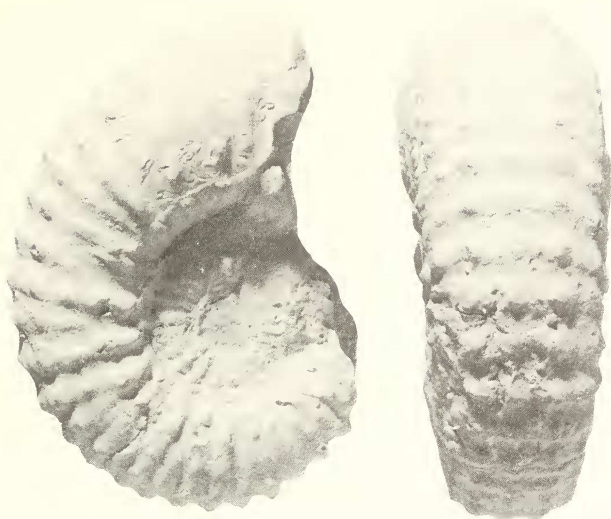
The *Romaniceras* from Texas described by Adkins (1931) are both synonyms of *R. ornatissimum*; *R. (Y.) loboense* Adkins (1931, p. 44, pl. 2, figs. 1, 21; pl. 3, fig. 5), is based on a poorly figured fragment; the holotype of *R. (Y.) cummingsi* Adkins (1931, p. 43, pl. 3, fig. 6) is an adult 330 mm in diameter.

Mantelliceras conquistador Anderson (1958, p. 245, pl. 15, fig. 2), *M. aff. conquistador* Anderson (1958, p. 245, pl. 14, fig. 2) and *R. hesperium* Anderson (1958, p. 246, pl. 23, fig. 1, 1a) are further synonyms based on Californian material, and are discussed by Matsumoto (1958, pp. 87-92).

Acanthoceras shastense Reagan (1924, p. 179, pl. 18, fig. 1; see Matsumoto 1959, p. 94, pl. 23, fig. 1a-c; pl. 24, figs. 2a-b, 3a-b; text-figs. 47-50) is a *R. (Yubariceras)* which occurs in the same member as *R. (Y.) ornatissimum* in California. It can be matched in the variants of *R. (Y.) ornatissimum* from Touraine which mature at a relatively small size and show an early decline of tubercles (e.g. de Grossouvre's *inermis*); as with the Touraine occurrence it is tempting to regard these as the microconch of the species.

The *Romaniceras* aff. *deverioides* of Reymont (1955, p. 46, pl. 9, fig. 1a-b) has nine rows of tubercles and the outer ventrolateral shows distinctive doubling, suggesting the specimen is an *Obiraceras*.

Occurrence. *R. (Y.) ornatissimum* is a typically mid Turonian species known from southern England; Sarthe, Touraine, and Vaucluse in France; the Lebanon; Israel; Tunisia; Madagascar; southern India; Japan; Mexico; and California and Texas in the United States.



TEXT-FIG. 9. *R. (Yubariceras) kanei* (Jones). Plaster cast of the holotype (Jones 1938, p. 120, pl. 8, figs. 7-8), University of Michigan collections no. 16819, from an unknown locality and horizon in Coahuila, Mexico.

CONCLUSIONS

From our study of the development and variation in more than 150 specimens of *Romaniceras* that we have seen, we suggest that the following species be recognized:

R. (Romaniceras)

1. *R. (R.) deverianum* (d'Orbigny)
2. *R. (R.) kallesi* (Zázvorka)
3. *R. (R.) pseudomphalum* (Matsumoto)
4. *R. (R.) fujishimai* (Matsumoto)

R. (Yubariceras)

1. *R. (Y.) ornatissimum* (Stoliczka)
2. *R. (Y.) kanei* (Jones)
3. *R. (Y.) aequicostatum* Matsumoto

R. (Obiraceras)

1. *R. (O.) ornatum* (Matsumoto)
2. *R. (O.)* sp. (= *R. aff. deverioides* and *R. uchauxiense* of Reyment, 1955).

Phylogeny and stratigraphy

Romaniceras evolved from *Kamerunoceras* (Kennedy and Wright 1979). The earliest known *Kamerunoceras* itself is from high in the Cenomanian of Devon (Bayliss collection) and is

morphologically intermediate between *Euomphaloceras septemseriatum* (Cragin) and *Kamerunoceras turoniense* (d'Orbigny) (= *K. salmuriense* (Courtiller)). *R. (Romaniceras) kallesi* is still similar to a *Kamerunoceras*, differing only in its nine rows of tubercles, of which those on the venter are even in strength, instead of irregular as in *Kamerunoceras*; nor is there ever any trace of a keel in *Romaniceras*. *R. kallesi* is found alongside *K. turoniense* in the St Cyr-en-Bourg Fossil Bed of Touraine, which yields a range of ammonites which together distinguish a *R. kallesi* assemblage-zone, probably equivalent to Zone 7 of Wiedmann (1960) in north Spain, somewhere in the middle of the Turonian stage (Hancock, Kennedy, and Wright 1977).

There is no stratigraphic evidence to support the statement of Cooper (1978, p. 104) that *R. (Yubariceras)* appeared in the 'Lower Turonian', nor that *Romaniceras* s.s. was derived from an early form of *R. (Yubariceras)*. The few records of 'Lower' Turonian *Romaniceras* are the result of the lack of standardization in the use of 'Lower', 'Middle', and 'Upper'. Thus Zázvorka (1958) records *R. kallesi* from the 'Lower' Turonian near Prague, but from the same area he also records *R. ornatissimum* from the lower part of the 'Middle' Turonian, the same stratigraphic order as is found in Touraine. Wiedmann (1960) recorded '*R. hispanicum*' from the 'Lower' Turonian of northern Spain, but the exact horizon of the specimen was actually unknown. The *Yubariceras* recorded by Collignon (1965, p. 24) from the 'Turonien inférieur' of Antsarona in Madagascar was associated with typical mid Turonian ammonites according to the list in Besairie and Collignon (1972, p. 281).

There is a stratigraphic gap in Touraine between *R. kallesi* and *R. deverianum* that is occupied by *R. (Y.) ornatissimum*. At present it is impossible to say whether *R. deverianum* is derived from *Yubariceras*, or whether it arose from *R. kallesi* in another region and then migrated back to western Europe. The succession in Japan fails to illuminate this point, but it is possible that Dr. W. A. Cobban's work on the Western Interior of the U.S.A. will give the answer.

Following de Grossouvre (1901) it has generally been assumed that *R. deverianum* marked the top zone of the Turonian, but in Touraine there are many minor disconformities between the horizon of *R. deverianum* and the overlying Coniacian. In England the few known *R. deverianum* come from below the Chalk Rock (Zone of *Subprionocyclus neptuni*) (Hancock, Kennedy, and Wright 1977). Thus the three species of *Romaniceras* described here all occur over a quite limited range within the middle of the Turonian stage, equivalent to the broad *Collignoniceras woollgari* Zone of authors.

R. (Y.) ornatissimum, the commonest and most widespread species of the subgenus, is found in Touraine stratigraphically between *R. kallesi* and *R. deverianum*. The records of Matsumoto (1975) shows that in Japan it ranges much higher. *R. (Y.) otatunei* extends from somewhere in the mid Turonian as high as the Zone of *Reesidites minimus*, now generally regarded as the highest zone of the stage. *Obiraceras ornatum* Matsumoto is probably also younger than any European *Romaniceras*.

There are no known descendants of *Romaniceras*.

Acknowledgements. We are grateful to the following colleagues for allowing us to examine specimens in their care, or for useful discussion: Dr. J. Sornay, Dr. D. Pajaud, the late General M. Collignon, Dr. R. Busnardo, Dr. J. P. Lefranc, Dr. J. Louail, Mme Baudouin, Mr. M. Gruet, Mr. Brulot, Mme de Sainte-Seine, Professor K. Young, Dr. C. Duerdon, Dr. M. R. Cooper, Dr. W. A. Cobban, Dr. W. A. Popenoe, Dr. E. G. Kauffman, Dr. V. Housá, Dr. R. Zázvorka, Dr. M. K. Howarth, Mr. D. Phillips, Professor T. Matsumoto, and Dr. I. Hayami. The financial support of the Royal Society, British Association for the Advancement of Science and N.E.R.C. is gratefully acknowledged by Kennedy and Hancock. We thank the staff of the Geological Collections, University Museum, Oxford, and in the Department of Geology, King's College, London, for their help and assistance.

REFERENCES

- ADKINS, W. S. 1931. Some Upper Cretaceous ammonites in western Texas. *Univ. Tex. Bull.* 3101, 35-72, pls. 2-5.
 ANDERSON, F. M. 1958. Upper Cretaceous of the Pacific coast. *Mem. geol. Soc. Am.* 71, 378 (+ xi) pp., 75 pls.
 ARKELL, W. J. *et al.* 1957. Cephalopoda Ammonoidea. *Treatise on Invertebrate Paleontology*, L, Mollusca 4, 490+xxii pp.

- BASSE, E. 1937. Les Céphalopodes Crétacés des massifs cotiers syriens 1. (Haut-commissariat de la République française en Syrie et au Liban.) *Notes Mém. Ht.-Comm. Syrie Liban* **2**, 165-200, pls. 8-11.
- BESAIRE, H. and COLLIGNON, M. 1972. Géologie de Madagascar. 1. Les terrains sédimentaires. *Annls. géol. Madagascar*, **10**, 59-109, pls. 1-11.
- COLLIGNON, M. 1939. Fossiles cénomaniens et turoniens du Menabe (Madagascar). *Annls géol. Serv. Mines Madagascar*, **10**, 59-105, pls. 1-11.
- 1965. *Atlas des fossiles caractéristiques de Madagascar (Ammonites)*, 12 (Turonien), 82 + iv pp., pls. 376-413.
- COOPER, M. R. 1978. Uppermost Cenomanian-basal Turonian ammonites from Salinas, Angola. *Ann. S. Afr. Mus.* **75** (5), 51-152.
- DIENER, C. 1925. *Fossilium Catalogus 1: Animalia*, 29 (Ammonoidea neocretacea), 244 pp. Berlin, Junk.
- FREUND, R. and RAAB, M. 1969. Lower Turonian ammonites from Israel. *Spec. Pap. Palaeont.* **4**, 83 + v pp., 10 pls.
- FRITSCH, A. 1872. *Cephalopoden der böhmischen Kreideformation*. 52 pp., 16 pls. Prague, the author.
- GROSSOURE, A. DE 1889. Sur le terrain crétacé dans le Sud-Ouest du bassin de Paris. *Bull. Soc. géol. Fr.* (3) **17**, 475-525, pl. 12.
- 1901. Recherches sur la craie supérieure 1: stratigraphie générale. *Mém. Serv. Carte géol. dét. Fr.* 1013 + vii pp.
- HANCOCK, J. M., KENNEDY, W. J. and WRIGHT, C. W. 1977. Towards a correlation of the Turonian sequences of Japan with those of north-west Europe. *Spec. Pap. palaeont. Soc. Japan*, **21**, 151-168.
- JIMBO, K. 1894. Beiträge zur Kenntniss der fauna der Kreideformation von Hokkaido. *Palaeont. Abh.* (N.S.) **2** (3), 147-194, pls. 17-25.
- JONES, T. S. 1938. Geology of Sierra de la Pena and paleontology of the Indidura Formation, Coahuila, Mexico. *Bull. geol. Soc. Am.* **49**, 69-150, pls. 1-13.
- JUIGNET, P. and KENNEDY, W. J. 1977. Faunes d'Ammonites et biostratigraphie comparée du Cénomani du nord-ouest de la France (Normandie) et du sud de l'Angleterre. *Bull. Soc. géol. Normandie*, **63** (2), 193 pp., 34 pls.
- KENNEDY, W. J. and HANCOCK, J. M. 1970. Ammonites of the genus *Acanthoceras* from the Cenomanian of Rouen, France. *Palaeontology*, **13**, 462-490, pls. 88-97.
- and WRIGHT, C. W. 1979. On *Kamerunoceras* Reyment, 1954 (Cretaceous Ammonoidea). *J. Paleont.* **53**, 1165-1178, 4 pls.
- KOSSMAT, F. 1895-1898. Untersuchungen über die Südindische Kreideformation. *Beitr. paläont. Geol. Öst.-Ung.* **9**, 97-203, pls. 15-25 (1895); **11**, 1-46, pls. 1-8 (1897); **11**, 89-152, pls. 14-19 (1898).
- KULLMANN, J. and WIEDMANN, J. 1970. Significance of sutures in phylogeny of Ammonoidea. *Paleont. Contr. Univ. Kans.* **47**, 32 pp.
- LECOINTRE, G. 1947. La Touraine. *Géologie rég. France*, **4**, 250 + ii pp., 4 pls.
- MATSUMOTO, T. 1959. Upper Cretaceous ammonites of California, part II. *Mem. Fac. Sci. Kyushu Univ. (D. Geol.)*, Special Vol. 1, 1-172, pls. 1-41.
- 1975. Additional *Acanthoceras* from Hokkaido (Studies of the Cretaceous ammonites from Hokkaido and Saghalien—XXVIII). *Mem. Fac. Sci. Kyushu Univ.* **22** (2), 99-163, pls. 11-23.
- SAITO, R. and FUKADA, A. 1957. Some *Acanthoceras* from Hokkaido (Studies on the Cretaceous ammonites from Hokkaido and Saghalien—XI). *Ibid.* **6** (1), 1-45, pls. 1-18.
- ORBIGNY, A. D' 1840-1842. *Paléontologie Française. Description des Mollusques rayonnés fossiles. Terrains Crétacés*, 1 (Céphalopodes), 662 pp., 151 pls. Paris, Victor Masson.
- 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés*. **2**, 428 pp. Paris.
- PERON, M. 1896-1897. Les ammonites du Crétacé supérieur de l'Algérie. *Mém. Soc. géol. Fr. Paléont.* **17**, 88 pp., 18 pls.
- PERVINQUIÈRE, L. 1907. Études de paléontologie tunisienne I. Céphalopodes des terrains secondaires. *Carte géol. Tunisie*, 438 + v pp., 27 pls.
- 1910. Sur quelques ammonites du Crétacé algérien. *Mém. Soc. géol. Fr. Paléont.* **17** (2-3), 86 pp., pls. 10-16.
- PICTET, F.-J. 1863. Mélanges paléontologiques. *Mém. Soc. Phys. Hist. nat. Genève*, **17**, 39 pp., 8 pls.
- REAGAN, A. B. 1924. Cretacic mollusca of Pacific slope. *Pan-Am. Geol.* **41**, 179-190, pls. 18-21.
- REYMENT, R. A. 1954. New Turonian (Cretaceous) ammonite genera from Nigeria. *Colon. Geol. Miner. Resour.* **4** (2), 149-164, 4 pl.
- 1955. The Cretaceous Ammonoidea of southern Nigeria and the southern Cameroons. *Bull. geol. Surv. Nigeria*, **25**, 112 pp., 25 pls.

- ROMAN, F. and MAZERAN, P. 1913. Monographie paléontologique de la faune du Turonien du bassin d'Uchaux et de ses dépendances. *Archs Mus. Hist. nat. Lyon*, **12**, 1-137, pls. 1-11.
- SHARPE, D. 1853-1857. Description of the fossil remains of Mollusca found in the Chalk of England. Cephalopoda. *Palaeontogr. Soc. (Monogr.)*, 68 pp., 27 pls.
- SOLGER, F. 1904. Die Fossilien der Mungokreide in Kamerun und ihre geologische Bedeutung, mit besonderer Berücksichtigung der Ammoniten. In ESCH, E., SOLGER, F., OPPENHEIM, M. and JAEKEL, O. *Beiträge Geologie von Kamerun*, 83-242, pls. 3-5.
- SPATH, L. F. 1923. On the ammonite horizons of the Gault and contiguous deposits. *Summ. Progr. geol. Surv. Lond.* for 1922, appendix 2, 139-149.
- 1926. On the zones of the Cenomanian and the uppermost Albian. *Proc. Geol. Ass.* **37**, 420-432.
- STOLICZKA, F. 1863-1866. Ammonitidae, with revision of the Nautilidae, etc. In BLANFORD, M. F. and STOLICZKA, F. 1861-1866. The fossil Cephalopoda of the Cretaceous rocks of southern India. *Mem. geol. Surv. India Palaeont. indica*, **1**, 41-216 + i-xii, pls. 26-94.
- THOMEL, G. 1972. Les Acanthoceratidae cénomaniens des chaînes subalpines méridionales. *Mém. Soc. géol. Fr. (N.S.)* **51** (mém. 116), 1-204, pls. 1-88.
- WEDEKIND, R. 1916. Über Lobus, Suturallobus und Inzision. *Zentbl. Miner. Geol. Paläont. (B)* **1916** (8), 185-195.
- WIEDMANN, J. 1960. Le Crétacé supérieur de l'Espagne et du Portugal et ses céphalopodes. *C.r. Congr. Socs sav. Paris Sect. Sci., Géol., Colloque sur le Crétacé supérieur français*, 709-764 (mis-dated 1959).
- 1964. Le Crétacé Supérieur de l'Espagne et du Portugal et ses céphalopodes. *Estudios geol. Inst. Invest. geol. Lucas Mallada* **1964**, 107-148.
- WRIGHT, C. W. and WRIGHT, E. V. 1951. A survey of the fossil Cephalopoda of the Chalk of Great Britain. Primarily a nomenclatorial revision of Daniel Sharpe's 'Description of the fossil remains of Mollusca found in the Chalk of England. Part I, Cephalopoda' (1853-1857). *Palaeontogr. Soc. (Monogr.)*, 40 pp.
- ZÁZVORKA, V. 1958. Acanthoceras kallesi n.sp. (Ammonoidea) ze spodního turonu na bílé hoře v praze (Střední Čechy) a Acanthoceras sharpei n.sp. z anglické Křidy. *Cas. národ. Mus.* **127** (1), 38-45.

W. J. KENNEDY, C. W. WRIGHT
University Museum
Parks Road, Oxford OX1 3PW
and Wolfson College, Oxford

J. M. HANCOCK
Dept. of Geology
King's College, Strand
London WC2R 2LS

Typescript received 28 March 1979

Revised typescript received 3 September 1979